# Assessing the effects of climate change on Baltic Sea macroalgae – implications for the foundation species *Fucus vesiculosus* L.

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**Academic dissertation**

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This thesis is a summary of the following articles, which are referred to by their roman numerals:

I **Takolander, A**., Cabeza, M. & Leskinen, E. 2017. Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review. *Journal of Sea Research* 123: 16-29

II **Takolander, A**., Leskinen, E. & Cabeza, M. 2017. Synergistic effects of extreme temperature and low salinity on foundational macroalga *Fucus vesiculosus* in the northern Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 495:110–8

III **Takolander, A**., Cabeza, M., Leskinen, E. 2018. Effects of ocean acidification on brown macroalga *Fucus vesiculosus* L. are small compared to seasonal changes in ecophysiology. *In revision.*

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| | I | II | III |
|---|---|---|---|
| **Original idea** | **AT*, MC** | **AT** | **AT** |
| **Designing the study** | **AT*, EL, MC** | **AT*, EL, MC** | **AT*, EL, MC** |
| **Literature search** | **AT*, EL** | **-** | **-** |
| **Conducting the experiment** | **-** | **AT** | **AT** |
| **Data analysis** | **AT** | **AT** | **AT** |
| **Writing the manuscript** | **AT*, EL, MC** | **AT*, EL, MC** | **AT*, EL, MC** |
| **Responsible for manuscript preparation** | **AT** | **AT** | **AT** |

*contribution > 80%. AT: Antti Takolander, MC: Mar Cabeza, EL: Elina Leskinen



## ABBREVIATIONS

OA = ocean acidification; PSII = Photosystem II, $F_v/F_m$ = maximum potential quantum yield of PSII; alpha = light-limited efficiency of photochemistry measured with chlorophyll fluorescence; ssrETR = steady-state electron transport rate through PS II; ETRmax = maximum electron transport rate; CCM = carbon concentrating mechanism; SDM = species distribution model.

**ABSTRACT**

Marine macroalgae are important foundation species on rocky shores. The large, habitat-forming species, in particular support a variety of associated flora and fauna. The Baltic Sea is naturally species-poor due to brackish water, and perennial, large macroalgae such as *Fucus vesiculosus* have high ecological importance and are characterized as foundation species in hard substrate bottoms. In the Baltic Sea, climate change has been predicted to result in elevated seawater temperatures, declining salinity, caused by increases in rainfall, coastal eutrophication and ocean acidification (OA). These changes may be harmful for macroalgae either directly or through interacting effects. This thesis investigates the potential effects of climate change on the Baltic macroalgae, focusing on the foundation species *Fucus vesiculosus.*

Several ecosystem-level effects emerge from the results of Chapter I. The predicted changes brought about by climate change, declining salinity, increasing eutrophication and more frequent heat waves will likely be highly harmful for perennial foundation species such as brown (e.g. fucoid) and red algae, and favour fast-growing, green filamentous species. This can cause alterations in rocky shore ecosystems especially in the northern areas of the Baltic Sea.

The experiments assessed in the systematic literature review of Chapter I allowed estimation of the fundamental abiotic niche of *F. vesiculosus* in relation to temperature and salinity. *F. vesiculosus* had a broad temperature optima for growth around 15 $^{o}$C. Growth rate declined in salinities under 20, which are prevalent in the Baltic Sea. The experiments assessed covered temperature and salinity conditions which are not found in the Baltic under present climate, but may occur in the future, and thus yield important information on potential responses of *F. vesiculosus* under climate change.

The experiments conducted in this thesis showed that the effects of short-term heat waves on *F. vesiculosus* were more severe under low salinity. Even short (8 days) exposure to high temperature (26 $^{o}$C or higher) was highly harmful, especially when the algae were at the same time exposed to low salinity (4 units) predicted for the future northern Baltic Sea. Some of the observed effects only emerged several days after heat exposure, which highlights the importance of including a monitoring period in experimental settings. Specimens from the two local populations sampled had different responses to temperature treatments, suggesting that in order to capture an ecologically realistic response, it is important to sample several sub-populations for experimental manipulations.

Ocean acidification had only a modest effect on *F. vesiculosus*. OA did not affect the growth rate of the algae but caused increases in carbon content and a decline in nitrogen content, mostly in winter. Experiments conducted in two seasons revealed high seasonal differences in all parameters measured, which suggests that in order to capture realistically climate change effects, experiments should be conducted in multiple seasons. This is especially important in environments with high seasonal fluctuations in abiotic conditions, such as the Baltic Sea.

This thesis has identified a number of methodological aspects in conducting climate change experiments on macroalgae. Experiments have highlighted the importance of assessing the effects of interactions between global change -related variables, which call for improvements in modelling projections of climate change for *F. vesiculosus*. Local *F. vesiculosus* populations residing in shallow bays, which may be subjected to short-term heat waves in the future, are vulnerable in the Northern parts of the Baltic Sea, as they are at the same time exposed to declining salinity brought about by climate change.

**TIIVISTELMÄ**

Makrolevät ovat meriekosysteemien kovien kalliopohjien avainlajeja, jotka tarjoavat elinympäristön suurelle joukolle muita lajeja. Murtovesi tekee Itämerestä luontaisesti vähälajisen, ja monivuotiset, suurikokoiset makrolevät kuten rakkolevä (*Fucus vesiculosus*), ovat siksi ekologisesti erityisen merkittäviä. Itämerellä ilmastonmuutoksen on ennustettu johtavan meriveden lämpenemiseen sekä sadannan kasvusta johtuvaan suolapitoisuuden laskuun. Näiden lisäksi ilmastonmuutos aiheuttaa meriveden happamoitumista sekä kiihdyttää rehevöitymistä. Nämä ympäristömuutokset voivat olla makroleville haitallisia erikseen tai yhdessä. Tämä tutkimus selvittää ilmastonmuutoksen vaikutuksia Itämeren makroleville, keskittyen erityisesti rakkolevään.

Kappaleen I tulokset viittaavat siihen, että ilmastonmuutos voi aiheuttaa huomattavia muutoksia Itämeren makroleväyhteisöjen rakenteessa. Ennustetut muutokset, kuten laskeva suolapitoisuus, etenevä rehevöityminen ja useammin esiintyvät korkeat lämpötilat ovat todennäköisesti haitallisia monivuotisille rusko- ja punaleville, ja suosivat nopeakasvuisia, rihmamaisia viherleviä. Tämä saattaa aiheuttaa huomattavia muutoksia Itämeren rantavyöhykkeen lajistossa, erityisesti Itämeren pohjoisosissa, joiden on ennustettu lämpenevän ja makeutuvan merkittävästi.

Kappaleen I kirjallisuuskatsauksessa läpikäytyjen artikkelien perusteella voitiin selvittää rakkolevän ekologinen lokero suhteessa lämpötilaan ja suolapitoisuuteen meta-analyysin avulla. Rakkolevällä on leveä kasvun lämpötilaoptimi 15 ºC molemmin puolin. Kasvunopeus heikkenee alle 20 yksikön suolapitoisuudessa, joka vallitsee esim. koko Itämeren alueella. Kirjallisuuskatsauksen esiin nostamat artikkelit kattoivat laajan lämpötila- ja suolapitoisuusarvojen yhdistelmän, joista kaikkia ei esiinny Itämerellä nykyisin, mutta jotka oletettavasti yleistyvät tulevaisuudessa ilmastonmuutoksen myötä. Tämän vuoksi niiden perusteella tehty meta-analyysi antaa arvokasta tietoa rakkolevän mahdollisia vasteita ilmastonmuutokseen.

Tässä väitöskirjassa toteutetut kokeet osoittivat jopa lyhytkestoisen (8 päivää) altistuksen korkealle lämpötilalle olevan rakkolevälle haitallista. Korkean lämpötilan (26 ºC tai yli) vaikutukset olivat erityisen haitallisia yhdistettynä alhaiseen suolapitoisuuteen (4 yksikköä), jollaista on ennustettu pohjoiselle Itämerelle vuosisadan loppuun mennessä. Osa havaituista vaikutuksista ilmeni vasta useita päiviä altistuksen jälkeen, minkä vuoksi on tärkeää sisällyttää ekologisiin kokeisiin riittävän pitkä tarkastelujakso kaikkien mahdollisten vaikutusten havaitsemiseksi. Kahdesta erillisestä paikallispopulaatiosta kerätyt yksilöt reagoivat lämpötilakäsittelyihin eri tavalla. Tämän vuoksi ilmastonmuutoksen vaikutuksia käsittelevissä kokeissa on tärkeää, että yksilöitä kerätään kokeeseen useista paikallispopulaatioista.

Merien happamoitumisen vaikutukset rakkolevään osoittautuivat vähäisiksi. Happamoituminen ei vaikuttanut rakkolevän kasvunopeuteen, mutta kasvatti leväkudokseen varastoituneen hiilen määrää, ja vähensi typen määrää, erityisesti talvella. Kaikissa mitatuissa fysiologisissa muuttujissa ilmeni huomattavaa vuodenaikaisuutta. Tämän vuoksi on tärkeää toteuttaa ilmastonmuutoksen vaikutuksia tutkivia kokeita useina eri vuodenaikoina, erityisesti Itämeren kaltaisissa elinympäristöissä, joissa ympäristön luontainen vuodenaikaisvaihtelu on suurta.

Tämä tutkimus on nostanut esiin useita menetelmällisiä kysymyksiä liittyen ilmastonmuutoksen vaikutusten tutkimiseen makrolevillä. Väitöskirjassa toteutetut kokeet alleviivaavat eri tekijöiden välisten yhteisvaikutusten tutkimisen tärkeyttä, mitkä huomioon ottamalla voidaan tuottaa tarkennettuja mallinnusennusteita ilmastonmuutoksen vaikutuksista rakkolevään. Ilmastonmuutoksen myötä yleistyvät äärilämpötilat ovat uhka matalissa lahdissa esiintyville rakkoleväpopulaatioille Itämeren pohjoisosissa, joissa suolapitoisuuden on ennustettu laskevan.

# SUMMARY

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## 1. INTRODUCTION

Climate change is one of the biggest present drivers of anthropogenic environmental change (Bellard *et al.*, 2012; Doney *et al.*, 2012), causing substantial changes in marine and terrestrial biological systems (Parmesan, 2006; Poloczanska *et al.*, 2013). Climate change has been observed to alter phenology, causing trophic mismatches (Edwards & Richardson, 2004; Parmesan, 2006), and alter the global distribution of biodiversity, as species track their thermal niches shifting towards the poles (Parmesan, 2006; Chen *et al.*, 2011). Further alterations in phenology (Pau *et al.*, 2011; Bellard *et al.*, 2012) and shifts in distribution (Cheung *et al.*, 2009; Kleisner *et al.*, 2017) have been predicted, with potential extinctions ensuing (Thomas *et al.*, 2004; Thuiller *et al.*, 2005).

Although ecological impacts of climate change in terrestrial ecosystems have been studied intensively, research in marine systems has lagged behind (Richardson & Poloczanska, 2008) due to limited data availability. The documented range shifts in marine environments are similar to those in terrestrial ecosystems (Poloczanska *et al.*, 2013), but potentially an order of magnitude larger (Sorte *et al.*, 2010; Poloczanska *et al.*, 2013, 2016; Straub *et al.*, 2016), as the species track their rapidly shifting local climatic conditions (Burrows *et al.*, 2011; Pinsky *et al.*, 2013; Molinos *et al.*, 2015). This emphasizes the importance of investigating the effects of climate change in marine ecosystems in detail.

Climate change has multiple dimensions, especially in marine systems (Doney *et al.*, 2012). Ecological effects of climate change are mediated through alterations in abiotic factors, such as temperature, salinity, pH and oxygen levels, interactions of these and other anthropogenic stressors (Doney *et al.*, 2012; Hillebrand *et al.*, 2018). Elevated temperature, driven by increased carbon dioxide concentration in the atmosphere, causes direct effects on biota. The rise in atmospheric $CO_2$ also intensifies the dissolution of $CO_2$ into seawater, causing Ocean Acidification (OA) (Orr *et al.*, 2005), with potentially severe ecological consequences (Fabry *et al.*, 2008; Feely *et al.*, 2009). Elevated temperature may cause alterations in regional precipitation and evaporation, altering the seawater salinity patterns (Meier *et al.*, 2011; Doney *et al.*, 2012). Salinity changes may cause substantial effects in coastal habitats, as salinity is one of the most important abiotic factors governing marine species distributions (Hällfors *et al.*, 1981; Lobban & Harrison, 1994; Vuorinen *et al.*, 2015).

Coastal macroalgae are important foundation species in the shallow bottoms which receive enough light for photosynthesis. Macroalgal beds are highly productive ecosystems, which harbour rich floral and faunal biodiversity (Kautsky *et al.*, 1992; Kersen *et al.*, 2011; Dijkstra *et al.*, 2012), and thus have high ecological importance. Climate change may affect the persistence and distribution of coastal macroalgae through alterations in multiple abiotic factors, such as temperature, nutrient availability, pH and salinity.

In this work, I investigate the potential effects of climate change on Baltic Sea macroalgae. The impacts of climate change in the Baltic Sea have been predicted to be particularly severe in

comparison to other large marine ecosystems. The Baltic Sea also is one of the few sea areas which have a comprehensive assessment of the expected magnitude and impacts of climate change (BACC Author Team, 2008; BACC II Author Team, 2015). From an ecological point of view, the Baltic Sea offers an interesting setting for climate change research, as the biota is under the strong influence of abiotic gradients, which are expected to be altered by climate change in the future. Effects of climate change on biodiversity are mediated through responses of foundation species, such as *Fucus vesiculosus*, which is the target species of this thesis (II, III).

## 1.1. CLIMATE CHANGE IN THE BALTIC SEA

The Baltic Sea is a shallow (mean 54 m), brackish water sea, characterized by a strong north-south salinity gradient, with the salinity levels in the Danish straits close to seawater, while the water in the farthest end of Bothnian Bay and Gulf of Finland is practically freshwater (Fig 1a, Myrberg *et al.*, 2006). The salinity gradient imposes strict restrictions on distribution of biota (Hällfors *et al.*, 1981; Snoeijs-Leijonmalm *et al.*, 2017), with the proportion of marine species higher in the southern area and replaced by freshwater species in the northern parts. Since brackish water is challenging for both marine and limnic species, the species diversity in the Baltic Sea is rather low, and the number of species decreases with declining salinity (Eriksson & Bergström, 2005; Schubert *et al.*, 2011; Snoeijs-Leijonmalm *et al.*, 2017).

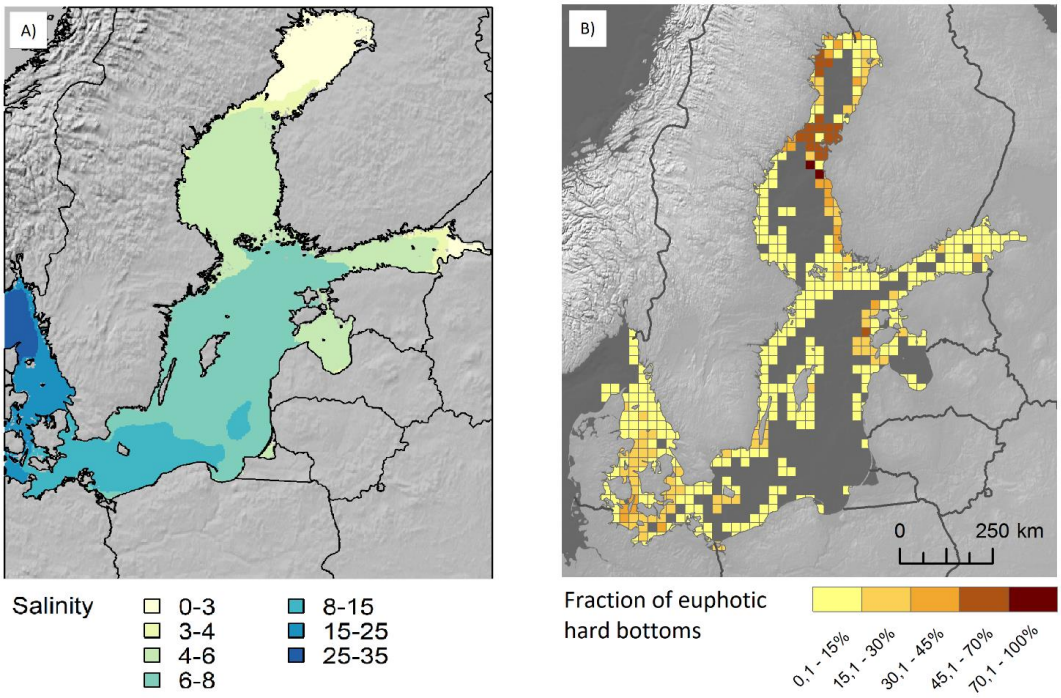


**Figure 1**. The current geographic distribution of surface salinity gradient in the Baltic Sea (a.), and relative abundance of euphotic hard bottoms (b.). Data from (a.) Hordoir *et al.* (2018) and (b.) HELCOM (2010).

Salinity conditions in the Baltic depend on riverine inflow of fresh water and inflow of saline water through Danish straits (Leppäranta & Myrberg, 2009; Snoeijs-Leijonmalm *et al.*, 2017). No clear long-term trend in salinity has been observed for the last hundred years (Winsor *et al.*, 2001; Fonselius & Valderrama, 2003), although large decadal oscillations exist. Nutrient concentrations have increased notably over the 20$^{th}$ century as a consequence of increased anthropogenic emissions (Fonselius & Valderrama, 2003; Andersen *et al.*, 2017), and eutrophication remains as one of the biggest environmental problems (Elmgren, 2001).

Small water volume makes the Baltic especially susceptible to warming, and the mean Sea Surface Temperature (SST) of the Baltic has increased rapidly during recent decades. During the last 30 years, the observed warming in the Baltic has been three to seven times higher than the global average, and the frequency of extreme temperatures has increased (MacKenzie & Schiedek, 2007; Belkin, 2009). Belkin (2009) identified the Baltic Sea to have the highest rate of observed warming of all the Large Marine Ecosystems of the World, with observed increase in mean SST of 1.35 $^{o}$C between 1982 and 2006.

The predicted rates of future warming in the Baltic are similarly high, with average SST increase of 2 – 3 $^{o}$C by 2100 (Meier, 2006). Higher rates of warming (4 $^{o}$C) have been predicted for the northern parts, especially the Gulf of Bothnia, while in the southern parts of the Baltic warming is expected to be more moderate (2 $^{o}$C) (HELCOM, 2013). In addition to mean temperature, also the frequency of extreme temperatures has been predicted to increase (Neumann *et al.*, 2012; BACC II Author Team, 2015).

Climate change has also been predicted to intensify the ongoing problem of coastal eutrophication in the Baltic Sea (BACC Author Team, 2008; BACC II Author Team, 2015). The predicted increases in precipitation increase runoff, which increases transport of nutrients from land to sea. Elevated temperatures favour cyanobacteria (Neumann *et al.*, 2012; O'Neil *et al.*, 2012), which contribute further to eutrophication by fixing atmospheric nitrogen. Elevated temperature also increases respiration rates and at the same time reduces solubility of oxygen in seawater. Increases in primary production, temperature and respiration may cause further deterioration of oxygen conditions in the Baltic Sea (Meier *et al.*, 2012a, 2012b; Neumann *et al.*, 2012). This may cause increased remobilization of nutrients from anoxic Baltic sediments, further increasing ongoing eutrophication (Pitkänen *et al.*, 2001; Vahtera *et al.*, 2007).

Elevated temperature has been predicted to decrease the sea ice extent by 60-80% by the end of the Century, and increase the duration of ice-free period (Meier, 2006; Neumann, 2010), which would result in increased light availability in the water column during winter.

In addition to elevated temperature, the salinity levels of the Baltic are predicted to decline in the future due to increased precipitation in the drainage area, consequently increasing freshwater input. The estimated decline in mean salinity is 2 to 3 units by the end of the Century (Meier 2006), shifting the salinity gradient southward (Vuorinen *et al.*, 2015). However, there is large uncertainty related to the accuracy of the salinity predictions (Meier *et al.*, 2006; HELCOM, 2013).

Higher precipitation has been predicted to cause increased nutrient input into the Baltic (Neumann, 2010; Meier *et al.*, 2012a), advancing eutrophication. In addition to precipitation, future nutrient emissions will depend on agricultural practices and dietary habits of the residents in the drainage area, as well as effectiveness and implementation of mitigation efforts such as the Baltic Sea Action Plan (Friedland *et al.*, 2012).

## 1.2. COASTAL MACROALGAE AS FOUNDATION SPECIES

Macroalgae are a polyphyletic group, which is usually divided into three groups: the red algae (*Rhodophyta*), the brown algae (*Phaeophyta*) and the green algae (*Chlorophyta*), a classification first based on the colour of photosynthetic pigments (Dring, 1992), and later phylogeny (Baldauf, 2003). Of these, green algae have high number of freshwater species, whereas brown algae, and especially red algae, reside mostly in marine habitats (Dring, 1992).

Macroalgae are foundation species in coastal ecosystems, maintaining biodiversity in rocky shores, which lack suitable substrate for aquatic vascular plants (Lobban & Harrison, 1994). Macroalgae increase habitat complexity by providing shelter for diverse faunal communities (Kautsky *et al.*, 1992) and form important habitat and breeding grounds for different fish species (Aneer & Nellbring, 1982; Anderson, 1994; Šaškov *et al.*, 2014). Macroalgal beds are among the most productive ecosystems on Earth (Costanza *et al.*, 1997), and constitute a substantial carbon sink from atmosphere into the deep sea floor (Krause-Jensen & Duarte, 2016).

The number of macroalgal species is highest in the southern Baltic, where the salinity is also highest, and it declines towards the north (Nielsen *et al.*, 1995), as marine species reach their tolerance limit in low salinity. On the other hand, the northern shoreline of the Baltic Sea is highly fractured (Winterhalter *et al.*, 1981), and thus hosts high potential as suitable macroalgal habitats in the form of euphotic hard bottoms (Fig. 1b). The macroalgal community in the northern Baltic Sea comprises of annual, filamentous algae and few large perennial species, such as *Fucus* spp., which have high ecological importance (Box 1, Kiirikki & Lehvo, 1997; Bergström & Bergström, 1999; Råberg & Kautsky, 2007; Wikström & Kautsky, 2007; Kersen *et al.*, 2011; Schagerström *et al.*, 2014).

**Box 1. *Fucus vesiculosus* – foundation species in rocky shores**

*F. vesiculosus* is the only large, widely dispersed perennial macrophyte in the brackish water of the Baltic Sea that provides year-round habitat for associated species. It creates a distinct habitat in shallow, hard bottoms (Fig. 2), which is important for a high number of flora and fauna. Several species of filamentous algae, such as *Ceramium tenuicorne*, *Elachista fucicola*, *Polysiphonia* spp. and Ectocarpales occur as epiphytes, growing on *F. vesiculosus*. The filamentous algae, and *F.vesiculosus* itself, are consumed by grazers, most importantly the isopod *Idotea balthica. F. vesiculosus* forms a distinctive vegetation zone and grows permanently submerged in the Baltic, in contrast to Atlantic populations. In brief, key aspects of *F. vesiculosus* are the following:

- A perennial species that provides habitat complexity, biomass and shelter throughout the year
- Important for invertebrates and juvenile fish
- Its depth penetration has declined in recent decades due to eutrophication

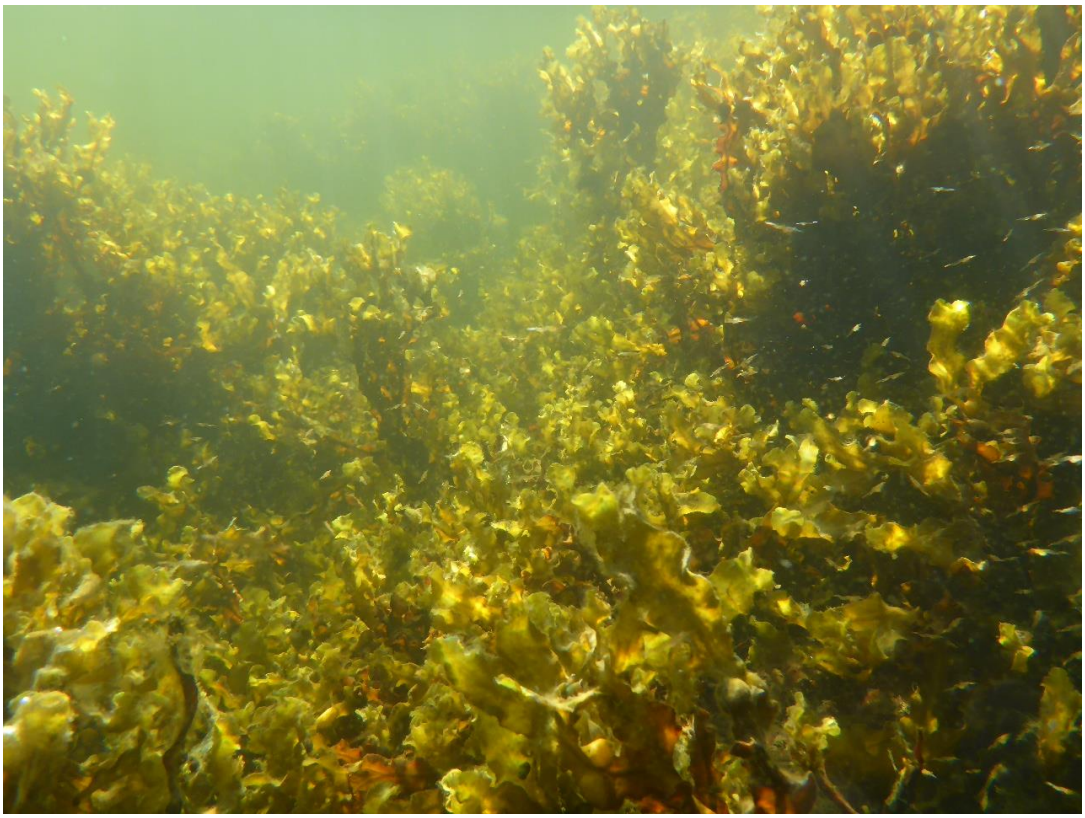

**Figure 2**. *Fucus vesiculosus* stand with a swarm of mysids swimming by in Hanko archipelago, SW Finland, at 1.5 meters depth, August 2014. Photo by Antti Takolander.

Annual, filamentous algae, such as *Ceramium tenuicorne*, *Cladophora glomerata*, *Ulva intestinalis* and *Pylaiella littoralis* form a belt in the littoral zone, closest to the surface (Waern, 1952). Below it in the sublittoral zone lies a *Fucus* belt, and further down with lower insolation a red algal belt (Waern, 1952; Kautsky *et al.*, 1992; Kiirikki, 1996, Fig. 3). This zonation creates a divergent ecological community, in which the filamentous algal belt is important for the juvenile stages of crustacean herbivores and detrivores, such as *Idotea* spp. and *Gammarus* spp., especially during summer (Kraufvelin & Salovius, 2004). Herbivores such as *Idotea* spp. migrate to *Fucus* zone during autumn (Salemaa, 1979).

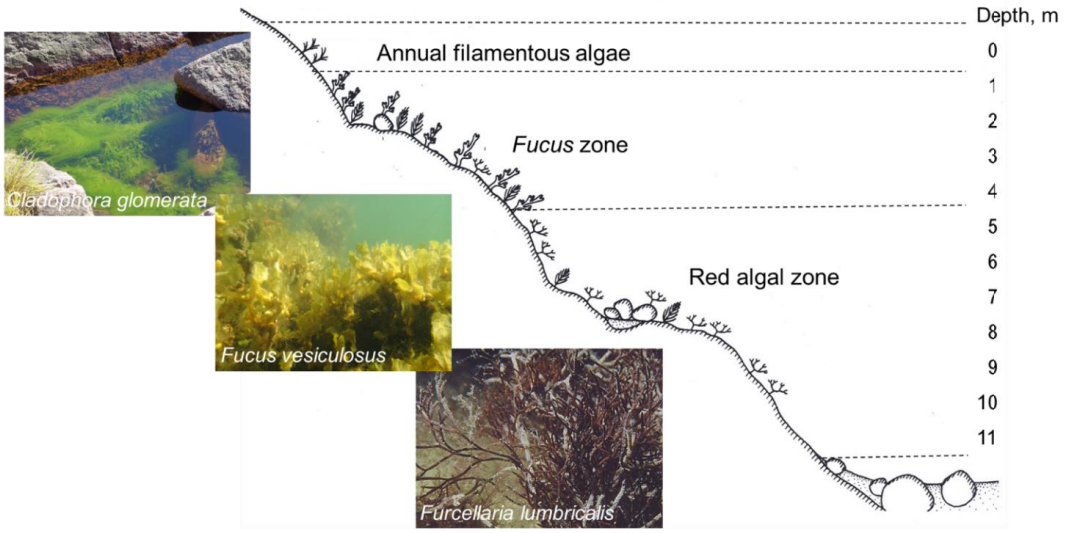


**Figure 3**. General zonation of macroalgal groups in northern Baltic rocky shores with species examples. Photos by Elina Leskinen.

## 1.3. MACROALGAE AND EUTROPHICATION

Since the 20th century eutrophication has greatly affected the macroalgal communities in the Baltic Sea. Excessive anthropogenic input of nutrients has favoured the growth of filamentous species, as these are able to utilize the excessive nutrients more rapidly than algae with larger fleshy thalli (Wallentinus, 1984a, 1984b; Kiirikki & Blomster, 1996), and also have higher photosynthesis rates (Leskinen *et al.*, 1992). Eutrophication has led to mass occurrences of attached and unattached filamentous algae, mainly of *P. littoralis*, *E. siliculosus*, *U. intestinalis* and *C. glomerata* (Bonsdorff *et al.*, 1997; Bäck *et al.*, 2000; Lehvo & Bäck, 2001). Overgrowth of filamentous algae has led to a decline in *Fucus* abundance in recent decades (Berger *et al.*, 2003; Råberg *et al.*, 2005). The abundance of filamentous algae also increases abundance of grazers, which may consequently exert negative effects on *Fucus* through increased grazing (Worm *et al.*, 1999; Engkvist *et al.*, 2000; Kotta *et al.*, 2000). Excessive growth of filamentous epiphytes also causes severe light limitation for their perennial host plant.

Eutrophication leads to decreased light availability in the water through higher growth of phytoplankton, which causes turbidity. As a result of light limitation the euphotic zone becomes narrower. Because of turbidity and epiphyte shading the deeper bottoms become unsuitable for attached photoautotrophs such as *F.vesiculosus* (Bäck & Ruuskanen, 2000; Torn *et al.*, 2006; Rohde *et al.*, 2008). In the Archipelago Sea, the total area of illuminated seafloor (area receiving > 1 % of surface photosynthetically active radiation, PAR) has declined 50% from 1930 to 2007 (Tolvanen *et al.*, 2013). Eutrophication also increases sedimentation, which has negative effects on perennial macroalgae, especially those growing in deep bottoms where wave action is low (Eriksson & Johansson, 2003, 2005). In consequence, the *Fucus* belt has shifted substantially towards the surface in the 20th Century (Kautsky & Kautsky, 1986), reducing the *Fucus* biomass at the same time.

## 1.4. CLIMATE CHANGE AND BALTIC MACROALGAL COMMUNITY

In addition to eutrophication, the future Baltic macroalgal communities will be affected by climate change. Effects of climate change are mediated through species-specific tolerances to changes in environmental factors, and these in turn will alter biotic interactions shaping the community composition (Parmesan, 2006; Blois *et al.*, 2013). Species may respond to environmental changes either through tolerance, adaptation, or migration (Bellard *et al.*, 2012). Tolerance may include behavioural, physiological or phenological changes within the tolerance limits of the organism (Pörtner & Farrell, 2008; Bellard *et al.*, 2012). As the pace of ongoing climate change may exceed the pace of environmental changes experienced by the biota earlier (Kemp *et al.*, 2015), the potential for adaptation of local populations may be exceeded (Torda *et al.*, 2017), especially in marginal habitats near abiotic tolerance thresholds (Hoffmann & Sgrò, 2011). Also quantitative evidence for genetic adaptation to climate change in natural populations remains scarce (Merilä & Hendry, 2014).

### *1.4.1. Effects of elevated temperature*

Temperature is the most important factor structuring the latitudinal distribution of macroalgae in oceanic areas (Lüning, 1984; Lüning *et al.*, 1990), with species-specific tolerance thresholds that relate to the completion of life cycle (Eggert, 2012). Globally, macroalgal distribution shifts towards poles have been observed (Wernberg *et al.*, 2011; Nicastro *et al.*, 2013) and predicted (Jueterbock *et al.*, 2013), as temperate species track their thermal regimes.

Many Baltic macroalgae are also found in the Atlantic, where they reside in cold/temperate regions with optimum temperatures for growth between 10 and 15 $^{o}$C (Fortes & Lüning, 1980). Some Baltic populations have been suggested to have lower temperature optima compared to the Atlantic (Nygård & Dring, 2008). In contrast to the Atlantic habitats, in the Baltic many originally intertidal species, such as *F. vesiculosus*, live permanently submerged, and thus are subjected to less severe temperature fluctuations.

Some of the Baltic macroalgae are arctic species, which may suffer from warming (Snoeijs, 1992a; Bischoff *et al.*, 1993; Wiencke *et al.*, 1993). However, a large fraction of Baltic macroalgae are Atlantic species that reside suboptimal temperature in the cold Baltic. Thus, for many of the species, moderate warming may improve growing conditions through lengthening of the growing season (Kotta *et al.*, 2014). Mild winters have been observed to lead to earlier reproduction of Baltic *F. vesiculosus* due to accelerated growth of receptacles (Kraufvelin *et al.*, 2012). Absence or reduction of sea ice may also favor *F. vesiculosus*, as it may potentially grow closer to surface in the absence of ice scraping, known to often detach the fronds from the bottom (Kiirikki, 1996).

In contrast to increasing mean temperature, short-term heat waves may be harmful for sessile organisms such as macroalgae, which reside near the surface, where water temperatures may surpass critical levels. Short-term extreme temperatures may have profound effects on species and ecosystems, as often the extremes rather than the average temperature have stronger effects on biological communities (Jentsch & Beierkuhnlein, 2008; Roth *et al.*, 2010; Grilo *et al.*, 2011). Globally, marine heat waves have caused range contractions and eliminated macroalgae populations regionally (Wernberg *et al.*, 2012a; Smale & Wernberg, 2013).

### *1.4.2. Effects of declining salinity*

Many Baltic macroalgae are originally marine or estuarine species, and have colonized the Baltic from the more saline Atlantic Ocean, subsequently adapting to low salinities (Russell, 1988, 1994). Despite adaptation, the critical occurrence threshold for many species with marine origin lies in salinities of 3-4 (Vuorinen *et al.*, 2015), and the location of this isoline has been predicted to shift

substantially towards south by the end of 21th Century (Meier, 2006). In macroalgae, low salinity may increase the frequency of a asexual reproduction (Tatarenkov *et al.*, 2005; Kostamo *et al.*, 2011; Forslund & Kautsky, 2013) alter the sex ratio (Serrão *et al.*, 1999) or decrease the size and change morphology of individuals (Ruuskanen & Bäck, 2002). Reproduction of *F. vesiculosus* fails in low salinities, since the male gametes lose their mobility (Serrão *et al.*, 1996). Also growth rates are negatively affected by low salinity (Rugiu *et al.*, 2018). Low salinity may cause shrinkages in geographic range of *F. vesiculosus*, and populations may be lost in the current northern edge of the distribution (Vuorinen *et al.*, 2015; Jonsson *et al.*, 2018, Box 2).

**Box 2. *Fucus vesiculosus* and climate change**

*F. vesiculosus* is originally a marine species, and although it can tolerate brackish water it is absent in very low salinities. *F. vesiculosus* reproduction fails in low salinity due to loss of mobility in male gametes. At the Finnish and Swedish coastal areas, the current edge of distribution lies in salinities of 3 to 4 units. If the salinity of the Baltic declines as predicted, the distribution of *F. vesiculosus* may contract towards the south. The Atlantic *F. vesiculosus* grows in the intertidal with high daily changes in temperature, while the permanently submerged populations in the Baltic are adapted to steady, seasonally changing temperature (0 – 20 ℃) and may thus be adversely affected by a rise in seawater temperatures. Eutrophication has entailed a general shift of the *Fucus* zone towards the surface, and it may be the primary cause of disappearances of some local populations. Climate change may intensify eutrophication through lengthening the growing season, and also increasing rainfall is expected to intensify nutrient runoff from land. Together these may lead to negative effects on the persistence of *Fucus* populations.

- Declining salinity may cause range contractions, especially at the northern distribution edge
- Reproduction fails in low salinity
- Has suffered from the effects of eutrophication
- High temperatures may be harmful

In areas, which become unsuitable for foundation species such as fucoids, adverse biodiversity consequences may emerge. Recently, a new fucoid species, *Fucus radicans*, was described in the Baltic Sea (Bergström *et al.*, 2005). *F. radicans* frequently reproduces asexually (Bergström *et al.*, 2005; Forslund & Kautsky, 2013). As *F. radicans* tolerates lower salinities than *F. vesiculosus* (Forslund *et al.*, 2012; Forslund & Kautsky, 2013; Leidenberger & Giovanni, 2015), it may replace the latter in some areas of the northern Baltic in the future. In areas of low salinity *F. radicans* reaches smaller size than *F. vesiculosus*, and because of this it has a lower biomass of associated fauna compared to *F. vesiculosus* (Schagerström *et al.*, 2014). This implies that even if fucoid persistence in areas of low salinity can be retained, the ecosystem functions provided be these species may be altered, if *F. vesiculosus* is replaced by *F. radicans*. The high rate of asexual reproduction has been suggested as an adaptive strategy (Forslund & Kautsky, 2013), but it decreases genetic diversity, which may affect population persistence in the long run (Johannesson *et al.*, 2011).

Potential future decline in salinities might alter the relative abundances of macroalgal species in large areas, but the exact effects depend on species-specific tolerances to low salinity. A relatively large proportion of green algae are freshwater species, and will manage in brackish water of very low

salinities (Bergström & Bergström, 1999). In a short-term experimental study, many green algae studied were unaffected by low salinity treatments, whereas the performance of brown and red algae was significantly poorer (Larsen & Sand-Jensen, 2006). Interestingly, the salinity tolerance of the species studied was relative to depth distribution in the field, with the species growing close to the surface generally having higher tolerance to low salinity.

### *1.4.3. Effects of ocean acidification*

When atmospheric carbon dioxide, $CO_2$, dissolves into seawater, the concentration of $H^+$ ions in seawater increases. This causes pH to decline, phenomena called ocean acidification (OA). In seawater, carbon dioxide forms carbonic acid ($H_2CO_3$), which dissociates into bicarbonate and carbonate, and free hydrogen ions (Box 3).

**Box 3. Components of the inorganic carbon system in seawater**

$$CO_{2(aq)} + H_2O_{(l)} \leftrightarrows H_2CO_{3(aq)}\ (carbonic\ acid)$$

$$H_2CO_{3(aq)} \leftrightarrows H^+_{(aq)} + HCO^-_{3(aq)}\ (bicarbonate)$$

$$HCO^-_{3(aq)} \leftrightarrows H^+_{(aq)} + CO^{2-}_{3(aq)}\ (carbonate)$$

Equations adapted from Fabry et al. (2008).

However, in addition to pH, OA also changes the relative abundances of dissolved inorganic carbon (DIC) components in seawater (Box 3, Fabry *et al.*, 2008). Under OA, the carbonate ($CO_3^{2-}$) pool will decline, whereas bicarbonate ($HCO_3^-$) and carbonic acid will increase, the latter having highest relative increase. In this thesis $H_2CO_{3(aq)}$ is referred to as $CO_2$, as $H_2CO_3$ immediately dissociates into $CO_2$ and $H_2O$. Key enzyme in carbon fixation by photosynthesis is Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase), which uses molecular $CO_2$ as carbon source. This means that the dissolved carbon in the $CO_2$ fraction in seawater can be directly utilized in photosynthesis by macroalgae (Raven & Hurd, 2012).

Although seawater hosts a substantial supply of inorganic carbon, in present-day seawater pH, majority of carbon is in the form of bicarbonate (Fig. 4), and only a small fraction is in the form of $CO_2$ (Raven *et al.*, 2008). The $CO_2$ diffusion rate in water is several orders of magnitude slower than in air, and hence many photoautotrophs would risk becoming carbon limited if they relied on passive diffusion of $CO_2$ alone. This is especially so in habitats such as dense macroalgal beds, where photosynthesis rates are high, resulting in high pH and low $pCO_2$ (Raven & Osmond, 1992; Middelboe & Hansen, 2007; Raven & Hurd, 2012; Koch *et al.*, 2013). To overcome carbon limitation, many species have evolved carbon concentrating mechanisms (CCMs), which concentrate molecular $CO_2$ near Rubisco. These mechanisms may include active transport of $HCO_3^-$, followed by intracellular dissociation of $HCO_3^-$ to $CO_2$, or passive diffusion of $CO_2$ into the cell after secretion of $H^+$ outside the cell wall to facilitate the dissociation of $HCO_3^-$ to $CO_2$ (Haglund *et al.*, 1992; Raven *et al.*, 2008, 2011).

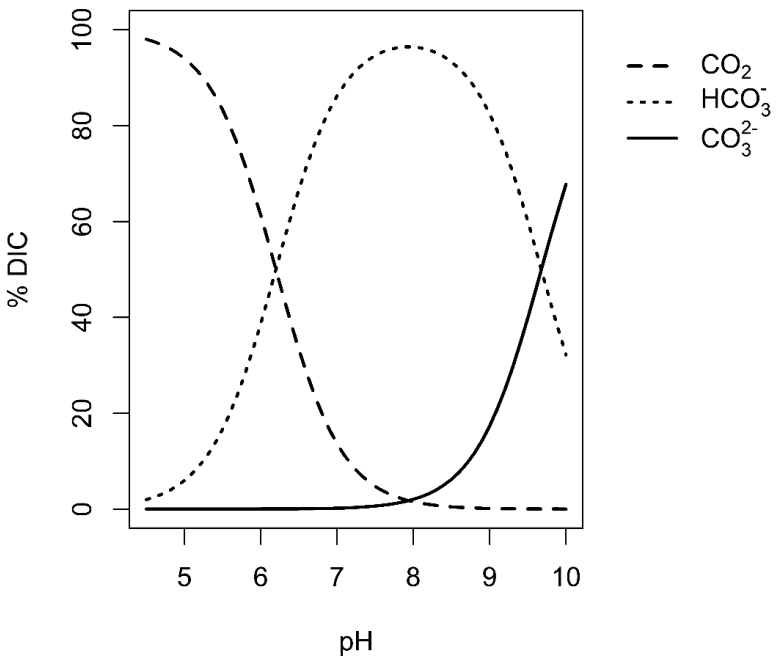


**Figure 4**. Relative proportion of $CO_2$, $HCO_3^-$ and $CO_3^{2-}$ of total dissolved inorganic carbon (DIC) under a range of pH values. Values have been calculated with r package "seacarb" (Gattuso *et al.*, 2015) with assumed 10 ºC temperature, 6 units salinity and 1400 µmol $l^{-1}$ alkalinity.

Ocean acidification has been suggested to favour macroalgae in the form of improved carbon availability (Koch *et al.*, 2013), which reduces energetic cost of carbon acquisition for photosynthesis as CCM activity may be downregulated (Raven *et al.*, 2011). If there is a large quantity of free $CO_2$ in the water, there is no need to use energy to run CCMs, and this could potentially save the energy and resources spent on CCM upkeep to be utilized elsewhere (Cornwall *et al.*, 2012; Raven *et al.*, 2014). However, CCM downregulation may also cause negative effects, since CCMs act as sinks for excessive light energy, and thus CCM downregulation may cause increased sensitivity to high light intensities (Liu *et al.*, 2012; Gao *et al.*, 2016), especially in algae growing near surface. Because of this, OA has been proposed to decrease marine primary production in future (Gao *et al.*, 2012). In either way, it is expected that the exact effects of OA on primary producers such as macroalgae, would depend on light availability (Verspagen *et al.*, 2014; Celis-Plá *et al.*, 2015). In experimental settings, free $CO_2$ usage has been observed to increase under OA treatments in species possessing CCMs (Cornwall *et al.*, 2012).

Under low irradiance, species with CCMs, which may also use free $CO_2$ as carbon source, may benefit from increased $CO_2$ availability brought about by OA. The opposite effect might emerge under high irradiance, if OA makes the algae more vulnerable to high irradiance. This way the expected effects of OA on macroalgae could be positive under low irradiance and negative under high irradiance. Experimental investigations on OA effects on macroalgae have yielded mixed results, as different species have exhibited variable responses (e.g. Israel & Hophy, 2002; Brading *et al.*, 2011; Fernández *et al.*, 2015; Nunes *et al.*, 2015), possibly due to differences in experimental design (Hurd *et al.*, 2009) or life history stages tested (Al-Janabi *et al.*, 2016a).

The Baltic Sea has high seasonal pH fluctuations (Omstedt *et al.*, 2010; Saderne *et al.*, 2013), which exceed the mean pH declines predicted by climate change. Especially large diurnal pH fluctuations, exceeding 1 unit, are observed in productive shallow environments such as macroalgal beds (Middelboe & Hansen, 2007). Since pH is frequently high in these habitats, they may mitigate OA effects on calcification by providing a refuge where calcification is possible (Wahl *et al.*, 2017). This emphasizes the importance of preserving viable populations of large perennial species such as *F. vesiculosus*. Eutrophication has increased seasonal pH fluctuations, with low pH occurring especially in winter, when primary production is low (Omstedt *et al.*, 2009). With the increasing atmospheric $CO_2$ levels, further declines in the mean pH as well as increased seasonal variability are expected (Schneider, 2011; Omstedt *et al.*, 2012). The alkalinity of the northern Baltic, especially Bothnian Bay and Gulf of Finland, is low, due to low alkalinity in the soils of the drainage area (Hjalmarsson *et al.*, 2008), which means that pH decline might be especially severe in these areas, as the buffering capacity of seawater is low.

*Fucus vesiculosus* has an effective CCM (Surif & Raven, 1989), and it is thus able to use $HCO_3^-$ as a carbon source for photosynthesis (Koch *et al.*, 2013), which is verified by the ability of *F. vesiculosus* to raise pH of the surrounding water, due to carbon uptake by photosynthesis. This occurs also in alkaline conditions (pH > 8) (Raven & Osmond, 1992; Middelboe & Hansen, 2007), when free dissolved $CO_2$ is mostly absent from the DIC pool (Fig. 4, Fabry *et al.*, 2008). Addition of DIC in experimental setting has increased photosynthetic oxygen evolution (Raven & Osmond, 1992), as well as electron transport rate and growth rate in *F. vesiculosus* (Nygård & Dring, 2008), which suggests that OA may be beneficial for *F. vesiculosus* (Box 4). However, such experiments are often conducted with fixed setting for other environmental variables, such as light. Light conditions in the future Baltic will likely deteriorate due to increased phytoplankton abundance, especially in the summer, if climate change increases primary production. On the other hand, an increase in ice-free days during winter will increase light availability, which may have substantial effects on the physiology of macrophytes (Kraufvelin *et al.*, 2012).

**Box 4. The potential effects of ocean acidification (OA) on *Fucus vesiculosus***

Ocean acidification is suggested to be beneficial for macroalgae because of improved carbon availability. This may yield some energetic advantages, if the algae downregulate the functioning of their carbon concentrating mechanisms (CCM), thus gaining energetic advantages. Experimental studies have given mixed responses, depending on experimental set-ups. *F. vesiculosus* has an effective CCM, which enables it to use bicarbonate, the most abundant form of inorganic carbon in seawater, as a carbon source for photosynthesis. The local *F. vesiculosus* populations in the northern part of distribution, Gulf of Bothnia, appear carbon limited in present seawater carbon concentrations. Thus OA might increase *F. vesiculosus* growth and photosynthesis. However, the effects of OA on macroalgae may also be negative because downregulation of CCM may make the algae more vulnerable to high irradiances.

- *F. vesiculosus* has an active carbon concentrating mechanism
- Photosynthesis of Bothnian Sea populations appear to be carbon limited
- Effects of OA on *F. vesiculosus* are mostly unknown

### *1.4.4. Interactive effects of climate change and coastal eutrophication*

Temperature in general has a substantial effect on the ecology of littoral zone, as both photosynthetic carbon fixation and respiration are temperature-dependent processes. Higher average temperature also means longer growing season (Kahru *et al.*, 2016), and may cause increased biological productivity in the littoral ecosystem. Case studies describing the ecological effects of thermal discharges of nuclear power plants indicate that in coastal areas, elevated seawater temperature promotes growth of filamentous algae, especially in eutrophic conditions, and leads to increased primary production (Ilus, 2009).

Growth of filamentous algae (Pajusalu *et al.*, 2013; Brodie *et al.*, 2014) and phytoplankton (Sommer *et al.*, 2015; Eberlein *et al.*, 2017) has been suggested to increase under ocean acidification. Thus OA and eutrophication may potentially drive the coastal ecosystems to the same direction, with potential negative consequences for perennial species such as *F. vesiculosus*, because both processes favor filamentous algae over perennial species. Some studies (Pajusalu *et al.*, 2013, 2016) suggest that because perennial species have lower metabolic rates, their primary production is not stimulated as much as that of filamentous, fast-growing species, which may express higher growth rates under OA (Olischläger *et al.*, 2013).

Although elevated temperature and OA may also favor the growth of perennial species such as *F. vesiculosus* (Kraufvelin *et al.*, 2012; Koch *et al.*, 2013), both processes may contribute to the ongoing coastal eutrophication, as both may be more favorable to fast-growing, opportunistic macroalgae, which exert negative effects on perennial species. Especially light limitation due to epiphytic shading, and increased grazing may cause rapid declines in regional abundance and depth penetration of *F. vesiculosus* (Kangas *et al.*, 1982).

## 1.5. COMMON METHODS USED IN ASSESSING CLIMATE CHANGE IMPACTS ON SPECIES, AND THEIR LIMITATIONS

The impacts of climate change on species are often assessed by experimentation or modelling, but rather seldom by a combination of these two. The two approaches can be considered somewhat contrasting. Spatial distribution modelling, which is often applied when studying range shifts induced by climate change, relies on long-term observational data on species distributions in the field, and links these to environmental variables expected to change in the future (Guisan & Thuiller, 2005; Elith & Leathwick, 2009).

In contrast, experimental investigations aim to disentangle the effects of single or few selected variables while holding other confounding factors fixed. Because of infrastructure and resources required, ecological experiments, especially in laboratory setting, are often of short duration compared to observational field studies (Forsman *et al.*, 2016). Possibly because of limited duration, many experiments only investigate the responses of a single stage of life history, since with most species a full completion of life cycle in a laboratory may be laborious or impossible. The environmental tolerances may vary at different life cycle stages (Eggert, 2012), and therefore short duration approaches may not fully describe the responses that would be expected to emerge in a species under future climate change.

Including interactions of several variables quickly increases the size of the experiment, why majority of laboratory experiments investigate effects of different variables in isolation (Wernberg *et al.*, 2012b). In consequence, variable interactions are often ignored, although these may have substantial

effect on performance of a species in natural settings (Wahl *et al.*, 2011). Experimental studies may also suffer from geographical or taxonomic biases. In a review of 110 marine climate change experiments, Wernberg et al. (2012b) found that three quarters of experiments focused on benthic invertebrates, and half of the experiments were conducted on temperate species. On local scale, biases may also occur if test organisms are harvested from single site, leaving the potential variability in responses of local populations unaccounted for.

Experiments of short duration often cover only single season, or a fraction of a season. In environments with substantial seasonal changes, inferences drawn from an experiment conducted in one season may not hold when extrapolated to other seasons (Boersma *et al.*, 2016). In contrast to laboratory experiments, observational field studies tend to have longer duration. Since they are conducted by observing the species in their natural setting, they may be considered ecologically more realistic, as they often incorporate natural environmental variability, multiple species, and cover several seasons (Forsman *et al.*, 2016). However, these types of studies are inherently correlational, since it is not straightforward to manipulate the variables of interest (but see Smale *et al.*, 2011; Pajusalu *et al.*, 2013; Wahl *et al.*, 2015). The results are hence based on naturally occurring gradients and range of data, which may be correlated with other abiotic or biotic variables, and may not cover the expected magnitude of future climate change, or the future combinations of different variables (Williams *et al.*, 2007).

After large datasets of both species distributions and environmental variables have become available, they have been widely used in studies applying spatial modelling such as Species Distribution Models (SDMs), which are perhaps the most widely used tools for predicting the effects of climate change on biodiversity (Elith & Leathwick, 2009). In SDM approach, a statistical model is built between spatial patterns of species presence or absence, or a combination of both, and spatial information about environmental variables that supposedly restrict the species' distribution (Thuiller *et al.*, 2008; Elith & Leathwick, 2009).

SDMs rely heavily on the concept of fundamental niche, originally proposed by G. Evelyn Hutchinson (Hutchinson, 1957), which is defined as the n-dimensional hypervolume of environmental space, where a species can exist indefinitely in the absence of competition. Even though data availability has made SDM modelling studies possible during recent years, the approach suffers from similar limitations as observational field studies. A major difficulty lies in estimating how geographic distribution relates to the fundamental niche dimensions (Araújo & Guisan, 2006). An assumption, that the distribution of a species investigated is controlled by the environmental variables, needs to be made (i.e. that the observed distribution corresponds to the fundamental niche), which does not necessarily hold in reality, as species distribution may be affected by other factors, such as dispersal limitation (Svenning & Skov, 2004; Guisan & Thuiller, 2005).

Second problem, prevalent when the SDMs are used in estimating the impacts of climate change, relate to extrapolation. The data range in present-day environmental conditions may not cover the expected future range of environmental variables, or their combinations (Williams *et al.*, 2007). In addition, the relationships established between species distributions and environmental variables may not hold in the future. Due to correlative nature of field observations, usually neither of these limitations can be addressed within the traditional SDM methodology.

Experimental manipulations may overcome some of these limitations, as they may target data range not covered by spatial data sets. This way it is possible to verify that the species investigated occupies the full extent of the fundamental niche, and that the spatial model thus truly captures the

physiological performance threshold of the species. Despite potential benefits, there have been very few attempts to combine these different approaches (but see Martínez *et al.*, 2015; Franco *et al.*, 2018). Combination of both data sources may yield more relevant and reliable estimations of the impacts of climate change on studied species.

## 1.6. AIMS OF THIS WORK

The aim of this work is to investigate the potential effects of climate change on Baltic Sea macroalgae. The species with especial importance in this thesis is *Fucus vesiculosus*, and the effects of multiple dimensions of climate change on *F. vesiculosus* are investigated in experimental settings. The study also aims to produce and gather data on the physiological performance thresholds (fundamental niche) of *F. vesiculosus* under various temperature and salinity conditions. More specifically, this thesis targets the following research questions:

### *1.6.1. Investigating the community level effects and tolerance thresholds of the ecologically most important species (Chapters I and II)*

Effects of climate change on ecological communities emerge through surpassing species-specific tolerance thresholds, which may lead to abrupt changes in community composition (Kardol *et al.*, 2010; Nicastro *et al.*, 2013; Liu *et al.*, 2017). Identifying this type of tipping points is of crucial importance in investigating the ecological responses to climate change. To identify the known physiological performance thresholds that might constrain the survival or performance of different species in the future, a systematic literature search was performed (Chapter I), and the upper temperature tolerance limit of northern Baltic *Fucus vesiculosus* was investigated in a laboratory experiment (Chapter II).

### *1.6.2. Determining the fundamental abiotic niche of F. vesiculosus in relation to temperature and salinity (Summary)*

Seawater temperature and salinity are major abiotic factors expected to change in the future Baltic Sea. To fully understand the expected responses of *F. vesiculosus* to these factors, the fundamental abiotic niche of *F. vesiculosus* in relation to temperature and salinity sensu Hutchinson (1957) was studied. This was done with a meta-analysis using literature surveyed in Chapter I, the experiments conducted in Chapter II and comparing the obtained responses with field data on *F. vesiculosus* occurrences. The analysis related to the fundamental niche are described only in the summary section of the thesis.

### *1.6.3. Investigating interactions between different dimensions of climate change on F. vesiculosus (Chapters II and III)*

Different dimensions of climate change may have unexpected outcomes, and their combined effects may exceed those acting in isolation (Wahl *et al.*, 2011). In the Baltic Sea, the interaction between temperature and salinity is especially important, as these two factors are key components in structuring the biota. Especially the combined effects of low salinity and short-term high temperatures on *F. vesiculosus* are unknown. Recently, the effects of elevated mean temperature of the growing season and the expected future low salinity was investigated (Rugiu *et al.*, 2018). However, responses to short-term high temperature may be very different from the responses of long exposure to more moderate temperatures. Chapter II investigates the effects of short-term heat wave on *F. vesiculosus* under low salinity conditions predicted for the future Baltic Sea.

The effects of ocean acidification on primary producers may depend on irradiance (Verspagen *et al.*, 2014; Celis-Plá *et al.*, 2015), because irradiance has a major role in photosynthesis and thus carbon sequestration. However, many experiments are conducted under fixed irradiance regimes, although light levels may substantially alter the responses of primary producers to OA (Hoppe *et al.*, 2015; Gao *et al.*, 2016). Especially high irradiance has been proposed to be harmful under OA (Gao *et al.*, 2012; Liu *et al.*, 2012). Chapter III studied the potential effects of ocean acidification on *F. vesiculosus* growth and ecophysiology under high and low irradiance regimes.

### *1.6.4. Studying the effects of ocean acidification on F. vesiculosus and seasonality of responses (Chapter III)*

Ocean acidification has been proposed to have beneficial effects for macroalgae through increased carbon availability, which may boost growth and photosynthesis. Yet, different species have shown variable responses (Pajusalu *et al.*, 2013; Fernández *et al.*, 2015). OA has been observed to have negative (Gutow *et al.*, 2014) and positive (Al-Janabi *et al.*, 2016b) effects on *F. vesiculosus* growth. Such differences may be seasonal (Al-Janabi *et al.*, 2016b) or arise from confounding factors such as irradiance (Gao *et al.*, 2012; Verspagen *et al.*, 2014; Celis-Plá *et al.*, 2015).

The Baltic Sea has substantial fluctuations in many environmental factors, most notably light, nutrients, temperature and pH (Myrberg *et al.*, 2006; Omstedt *et al.*, 2009). To be able to estimate the responses of perennial species to future changes brought about by climate change, consideration should be made regarding in which season the experiments should be conducted, and how the results should be interpreted. Importantly, the biota of the Baltic has adapted to fluctuating environment, and many species such as fucoids show strong seasonality in their physiology (Lehvo *et al.*, 2001). It is worthy to note that the majority of marine climate change experiments are of short duration, and thus do not encompass multiple seasons (Forsman *et al.*, 2016, but see Werner *et al.*, 2016a). To quantify seasonal responses to OA, experiments in Chapter III were conducted in two seasons, winter and summer.

## 2. METHODS

### 2.1. SYSTEMATIC LITERATURE SEARCH (CHAPTER I)

In chapter I, a systematic literature review was carried out to survey the existing literature on the effects of altered temperature, salinity, carbon, and nutrient conditions on the most ecologically relevant macroalgal species. Since many of the Baltic macroalgae originate from the Atlantic, the differences between these two regional populations have been the subject of many comparative experiments. The focus of such experiments has been to investigate, if the Baltic populations have adaptations that allow them to persist in different environmental conditions than the Atlantic populations (e.g. Thomas *et al.*, 1989; Bäck *et al.*, 1992). Although not directly addressing the performance under future climate change, such knowledge can be potentially valuable in investigating the known tolerance limits of the most intensively researched species.

A systematic literature search was performed in fall 2016. The geographic focus of the investigation was on areas of the northern Baltic, which are expected to undergo major abiotic changes due to climate change in the future (Meier, 2006; BACC II Author Team, 2015), causing substantial restructuring of the biota (Vuorinen *et al.*, 2015). The species targeted were selected using the distributional species check list of Nielsen *et al.* (1995). To focus on species with highest ecological

importance, we selected the species listed as "dominant" or "frequent" in the northern Baltic, more specifically the Baltic Proper, Gotland Sea, Estonia, Åland Sea, Archipelago Sea, Gulf of Finland and Gulf of Bothnia. Two frequently occurring *Cladophora* species were added to the list together with *Fucus radicans*, which was not acknowledged as a separate species at the time the study of Nielsen et al. (1995) was compiled. After these additions, the total number of species amounted to 31.

A literature search from ISI Web of Knowledge was performed using the scientific species names with the following keywords: "temperature", "heat shock", "salinity", "osmotic stress", "nutrients", "eutrophication" and "ocean acidification" as the topic field. Besides that, a less systematic search was conducted in Google Scholar with the same search criteria to ensure that the full scope of existing literature was captured. These search criteria yielded 3042 papers. Of these, 128 studies dealt with the four variables investigated.

As the papers retrieved used wide range of methods and quantified the observed responses in different ways, observed responses were classified in four categories: "beneficial", "potentially beneficial", "tolerant" and "harmful" in relation to the four variables investigated. A salinity threshold of 4 units was used as a threshold for "low salinity", since it is the extreme distribution limit for many marine species (Vuorinen *et al.*, 2015). Declining salinity was classified as "harmful", if declining performance (decline in photosynthesis, survival or growth) or declining abundance in the field was observed under 4 salinity units, "tolerant" if no changes were recorded, and "beneficial" if a positive response was observed. Responses to temperatures were classified similarly, although no specific temperature threshold was used. The observed responses were evaluated in relation to expected temperature changes in the study area. Similarly, responses to ocean acidification were classified, but as some of the studies revealed ambiguous responses, also a fourth category "potentially beneficial" was used. In the case of OA, no threshold was used. If effects on performance (growth, photosynthesis, etc.) in the laboratory were observed when adding $CO_2$ or DIC, or if field observations revealed changes in abundance under low pH, the responses were classified into the categories mentioned above. The responses to eutrophication were mostly observed in field studies. Eutrophication was classified as "harmful" if the abundance in the field declined or shifted closer to surface under eutrophic conditions, "tolerant" if no effect was observed, and "beneficial" if eutrophication clearly increased the species abundance.

## 2.2. QUANTIFYING THE FUNDAMENTAL NICHE OF F. VESICULOSUS THROUGH EXPERIMENT AND FIELD DATA (SUMMARY)

The analyses presented in this section are an independent assessment, and the results are only presented in the summary part of the thesis, not in any Chapter. This section builds upon work conducted in Chapters I and II. The aim of this analysis was to estimate the temperature and salinity optimas and performance thresholds for *F. vesiculosus* through a meta-analysis, and to compare the obtained information with temperature and salinity responses obtained through field observations of *F. vesiculosus* occurrence.

### *2.2.1. Experiment data*

The experimental data was derived from studies identified in Chapter I, which investigated the responses of *F. vesiculosus* to different temperature and salinity conditions in laboratory settings. Parameter values describing fitness (growth rate or electron transport rate), and treatment levels were extracted from figures of published papers using online software WebPlotDigitizer (Rohatgi, 2011). In addition, also data gathered in Chapter II was used. Since the different experiments had varying

settings, and they were conducted under different seasons, the response variables measured were standardized to range from 0 to 1, so that the maximum value in the data set corresponded to 1. 0 was chosen as the lower limit for the scaling, as all the parameters measured in the experiments (growth rate or electron transport rate) had a natural lowest value at 0. In few cases where growth rates were negative, indicating tissue necrosis (e.g. Chapter II) the negative values were set to 0.

### *2.2.2. Field observations and model data*

Observations of *Fucus vesiculosus* distribution in the Baltic Sea were downloaded from HELCOM data portal. The HELCOM HOLAS II dataset (HELCOM, 2017) contains *Fucus* spp. presence/absence observations on a 5 x 5 km grid, and it is a combination of distribution data from various monitoring programs of HELCOM member countries (see http://maps.helcom.fi for detailed description). Some of the data sets do not necessarily distinguish between *F. vesiculosus* and *F. radicans*, hence it is possible that our distribution data also contains *F. radicans* observations.

The temperature and salinity data were obtained from the Nemo-Nordic ocean model (Hordoir *et al.*, 2018). Temperature data consisted of mean summer (June-July-August, JJA) temperature, which is the season of the most rapid growth in *F. vesiculosus* (Lehvo *et al.*, 2001). The salinity values used were mean annual seawater salinity. For both variables, means for 1995-2013 were calculated from the model predictions. The *F. vesiculosus* observation data was combined with temperature and salinity data layers by re-projecting the observation data layer in r using nearest neighbor estimation to compute values for new raster cells (Hijmans, 2016). Although the temperature and salinity values linked to *F. vesiculosus* field observations originate from an ocean model, these are referred to as "field data" in the Summary for the sake of clarity.

## 2.3. DESCRIPTION OF EXPERIMENTAL DESIGNS (CHAPTERS II AND III)

Experiments in Chapters II and III were conducted at Tvärminne Zoological Station (TZS), southwestern Finland. Mature *F. vesiculosus* thalli were used in both experiments. Algae specimens were harvested either using a rake or snorkeling from nearby populations, and only vegetative tips of the thallus free of epiphytes were used for the experiments.

### *2.3.1. Synergistic effects of high temperature and low salinity (Chapter II)*

The effects of short-term high temperature and low salinity, and their interaction, on survival and performance of *F. vesiculosus* were investigated in experimental settings in August 2015. Although earlier studies suggest that both factors have negative effects on *F. vesiculosus* performance, the aim of Chapter II was specifically to investigate their simultaneous effect, whether exposure to low salinity predicted for the future northern Baltic would make *F. vesiculosus* more vulnerable to high temperature. The experimental algae were harvested from two sites with different prevailing temperatures (difference approx. 2 $^{o}$C, Fig. 5 inset) to detect potentially different responses arising from acclimation to specific temperatures.

The harvested thalli were placed in 1 liter glass jars with two salinity levels, 4 ("low salinity") and 6 ("ambient salinity"). A salinity level of 4 represents the future salinity conditions expected to occur in the study area by the end of the Century (Meier, 2006; Neumann, 2010; Vuorinen *et al.*, 2015). The jars were placed in temperature-controlled water baths with continuous aeration. After an initial acclimation period of 4 days, the individuals were subjected to short-duration (8 days) high temperature, ranging from 20 to 28 $^{o}$C (Fig. 5). The high temperature treatment was followed by 11

days recovery period, in temperatures which corresponded to ambient seawater temperature at the study area during the experiment (Fig. 5).

In shallow coastal areas of the northern Baltic, thermal stratification in summer may increase water temperature rapidly in the surface water above the thermocline, where *F. vesiculosus* resides. Near TZS, temperature increases of 10 ºC have been observed in the course of few days (Haapala, 1994) in summer when thermal stratification develops. Current summer seawater temperatures reach 23 ºC in shallow (2m) bay (Krogarviken) next to TZS (FMI, 2016). Given the rapid rate of observed warming (MacKenzie & Schiedek, 2007; Belkin, 2009) in the Baltic, and the predicted rates of future warming and increased magnitude and frequency of extreme temperatures (Meier, 2006; Neumann *et al.*, 2012), the temperature treatments represent the future conditions the *F. vesiculosus* populations in shallow bays will likely be exposed to.

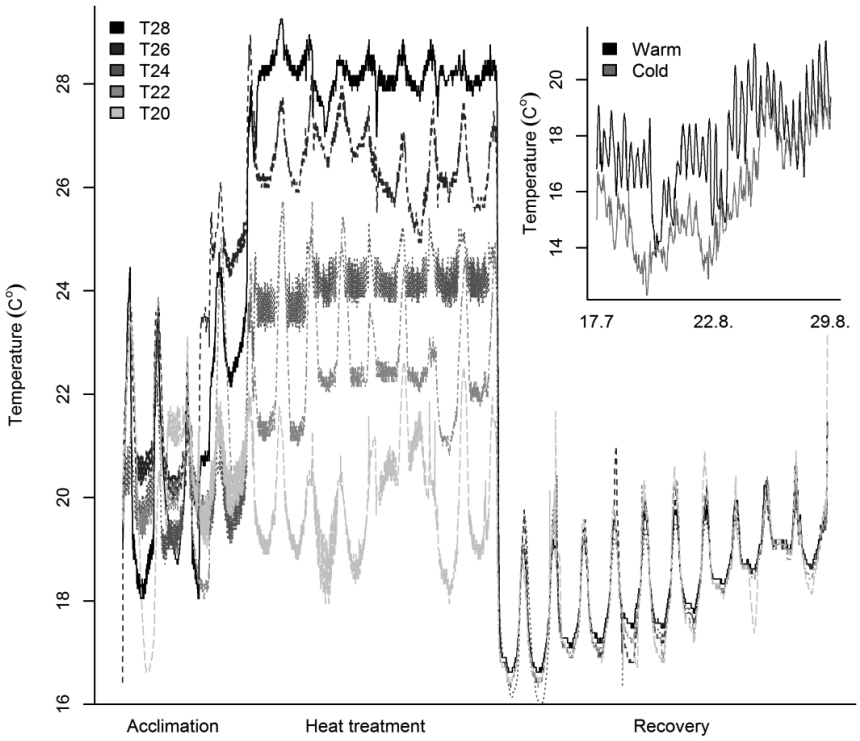


**Figure 5**. Temperature treatments during the Chapter II experiment. *F. vesiculosus* specimens were exposed to five temperature treatments (T20 – T28) for 8 days, followed by 11 days recovery period. The logged seawater temperatures from the two sites where the specimens were collected are shown in the inset.

Growth rate (increase/decrease in fresh weight, mg) and several chlorophyll fluorescence parameters, $F_v/F_m$, rapid light curves and steady-state electron transport rate (ssrETR) were measured at the end of the heat treatment and after the recovery period. A description of chlorophyll fluorescence methodology and ecological interpretation of chlorophyll fluorescence parameters is given in section 2.4. After the recovery period, the specimens were collected and frozen for later determination of the

mannitol content. Declining salinity changes the osmotic pressure, and algae tissue subjected to low salinity may absorb water. To ensure the validity of growth rate calculations using fresh weight, we also measured growth rate as length (mm precision), but as these two provided identical information, the former was used in the analysis.

### *2.3.2. Interactive effects of ocean acidification and irradiance (Chapter III)*

Effects of ocean acidification on *F. vesiculosus* under two different irradiance regimes was studied in two experiments, which were conducted in November-December 2015 (winter experiment) and June 2016 (summer experiment). As the effects of OA on macroalgae may depend on irradiance (see section 1.4.3.), the purpose of the experiments was to investigate a potential interaction between OA and irradiance. *F. vesiculosus* has highly seasonal physiology, storing carbon and nitrogen internally (Lehvo *et al.*, 2001). The responses could therefore differ by season, and inferences on OA effects could be potentially erroneous, if based only on experiments conducted in one season. Thus, the experiment was conducted in two seasons with different environmental conditions.

The algal specimens were placed in three OA treatments under two irradiance levels. Effects of OA were simulated by bubbling gaseous $CO_2$ into seawater using pH computers (AB Aqua Medic GmbH). $CO_2$ bubbling was conducted in header tanks, from which a constant flow-through of 80 ml/min supplied water to experimental jars (V = 1l) where the thallus tips were placed. The water flowing into header tanks was pumped from a bay next to TZS. In the winter experiment, one individual thallus sample was placed in each jar, whereas in the summer experiment, three marked individuals were placed in the same jar.

The levels of $CO_2$ partial pressure ($pCO_2$) in the OA treatments were: 'ambient' (236 µatm or 512 µatm, summer/winter), 'high' (1582 µatm or 2263 µatm, summer/winter) and 'very high' (4673 µatm or 7074 µatm, summer/winter). The light levels were 165 µmol photons $m^2s^{-1}$ and 81 µmol photons $m^2s^{-1}$ (winter) and 198 µmol photons $m^2s^{-1}$ and 131 µmol photons $m^2s^{-1}$ (summer) for high and low light treatments. The purpose of the light treatments was to investigate the effects of OA under high and moderate irradiance. The duration of the experiments was 18 (winter) and 22 days (summer). pH, salinity and temperature were monitored every 2$^{nd}$ or 3$^{rd}$ days throughout the experiment. The nutrient levels were measured from the inflowing seawater by TZS laboratory. Dissolved inorganic carbon was measured with a carbon analyzer Elektro-Dynamo URAS-3E, with a method described by Salonen (1981). $pCO_2$ levels and parameters of the seawater carbonate system were calculated from pH, salinity, temperature and DIC data using r package "seacarb" (Gattuso *et al.*, 2015).

In order to quantify the responses of *F. vesiculosus* photobiology to OA/irradiance treatments, we measured maximum potential quantum yield, $F_v/F_m$, and calculated several Rapid Light Curve parameters: the light-limited efficiency of photosynthetic light usage (alpha) and maximum relative electron transport rate (rETRmax), which describes the maximum rate of electron transport under high irradiance. All chlorophyll fluorescence parameters were measured at the end of the experiments. In addition, the fresh weight (mg) and length (mm) of all individual samples were recorded, after which the samples were frozen for further laboratory analysis. In the laboratory, carbon and nitrogen content were determined from defrosted samples using LECO TruSpec Micro CHNS. Chlorophyll *a* and *c* were extracted from grounded samples with ethanol, and absorption spectra was measured with a spectrophotometer (nm precision). Chlorophyll *a* and *c* contents were calculated using equations of Ritchie (2008).

## 2.4. CHLOROPHYLL FLUORESCENCE: SCREENING OF PHOTOSYNTHESIS *IN SITU* (CHAPTERS II AND III)

Chlorophyll fluorescence is a powerful, non-intrusive tool to measure photosynthetic activity. It is based on a model of three competing pathways for light energy absorbed by Photosystem II (PSII): photosynthesis, heat loss and fluorescence (Maxwell & Johnson, 2000). Commercial fluorometers available measure the fluorescence signal from PSII, which splits water to draw electrons, and releases oxygen. In a typical measurement, the electron transport chain (photochemistry) of PSII is fully reduced by application of a brief, saturating light pulse, and fluorescence is measured using modulated light. The short duration of saturating light ensures that the heat loss during measurement remains constant, and when the electron transport chain is fully reduced, photochemical energy conversion equals zero. By definition if either photochemistry or heat dissipation increases, fluorescence signal shows a decline. Thus changes in fluorescence yield, when measurements prior and during the pulse are compared, can give quantitative information on photochemical energy conversion (Baker, 2008).

The relative quantum yield of fluorescence is determined from fluorescence yield before and after administration of a saturating light (Genty *et al.*, 1989). If photorespiration is zero, quantum yield of fluorescence should show a linear relationship with $CO_2$ assimilation near Rubisco (Baker, 2008), however, this is not always the case, as electrons may also be captured by other sinks than $CO_2$ assimilation (Beer & Axelsson, 2004; Baker, 2008). When quantum yield is multiplied by photosynthetically active irradiance (PAR) absorbed by PSII, the electron transport rate through PSII may be calculated. In most cases under moderate irradiances, ETR can approximate $O_2$ production reasonably (Beer & Axelsson, 2004) and thus can be utilized in measuring efficiency of photosynthetic energy capture in plants and algae (Suggett *et al.*, 2010) (but see Franklin & Badger, 2001; Nielsen & Nielsen, 2008).

A common protocol to estimate the state of photosynthetic machinery is the rapid light curve (RLC) protocol (White & Critchley, 1999; Ralph & Gademann, 2005). In a RLC measurement, a sequence of fluorescence yield measurements are conducted under increasing irradiance. ETR values are calculated from fluorescence measurements, and when ETR is plotted against irradiance, a general declining shape is observed (Fig. 6). When irradiance is low, ETR (and photochemistry) is limited by light availability, and ETR increases linearly by irradiance. Under moderate irradiance, the linearity starts to break, as the enzymatic steps of $CO_2$ assimilation and associated processes limit the rate of oxidation/reduction of electron transport chain, until maximum ETR is achieved, often followed by decline in very high irradiances.

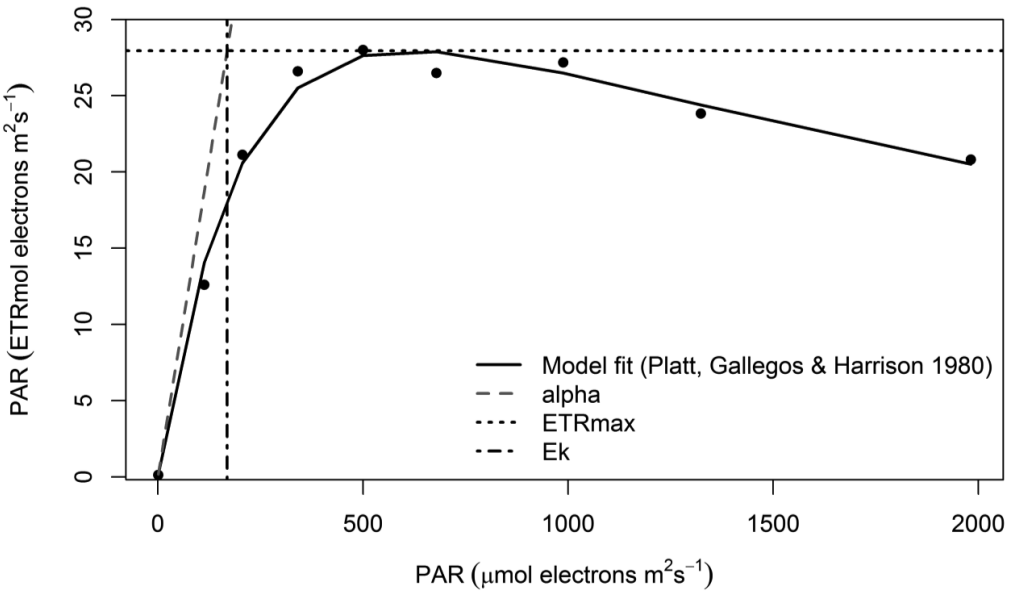


**Figure 6**. A rapid light curve measured from *F. vesiculosus* thalli by a scuba diver in approximately 2 m depth in outer archipelago of Hanko, July 2017. The dashed lines indicate the model parameters calculated: alpha, ETRmax and Ek. The duration of light increments was 20 seconds. PAR = photosynthetically active radiation.

Quantitative description of the curve by fitting a mathematical model (e.g. Platt *et al.*, 1981; Eilers & Peeters, 1988) allows evaluation of a set of parameters with physiological interpretation. A commonly used set of parameters is as follows: alpha, ETRmax and Ek. Alpha indicates the linear slope of the curve in light-limited region (Fig. 6), which in low irradiance correlates closely with maximum potential quantum yield of fluorescence. ETRmax is the maximum electron transport rate attained during RLC measurement. Ek is the minimum saturating irradiance, defined as intersection of alpha and ETRmax (Ralph & Gademann, 2005). It has been shown that under low to moderate irradiance electron transport rates correlate closely with $O_2$ production (Henley, 1993; Beer & Axelsson, 2004). RLC methodology and derived parameters can give rapid indication of the status of photosynthetic machinery (Serôdio *et al.*, 2006; Houliez *et al.*, 2017).

In RLC measurement the duration of illumination at different irradiance levels of a light curve is relatively short, often 10 – 20 seconds (Ralph & Gademann, 2005) which means that photosynthetic steady-state is not attained, in contrast to traditional photosynthesis-irradiance curve. The steady state here refers to a condition when fluorescence signal does not change under illumination, and thus heat transfer and photochemistry are constant. Some commercial devices can be set to perform fluorescence yield measurement after several minutes of illumination using an internal halogen lamp, which may be sufficient to attain photosynthetic steady state, allowing a measurement of ETR in photosynthetic steady state (in this thesis abbreviated ssrETR).

RLC parameters, together with measurements of maximum potential quantum yield ($F_v/F_m$), have been widely applied in stress physiology studies of aquatic primary producers, especially seagrass and macroalgae (see e.g. Suggett *et al.* 2010 and references therein). Especially $F_v/F_m$ has been

considered a good indicator for various aspects of physiological stress, such as harmful thermal and osmotic conditions (Ralph, 1998a, 1998b).

Chlorophyll fluorescence parameters were used to quantify the responses of *F. vesiculosus* photosynthetic machinery to experimental treatments in chapters II and III.

## 3. RESULTS

The experiments and analyses conducted in this thesis yielded novel information on climate change impacts on Baltic macroalgae. Most importantly, several processes were identified in Chapter I which may promote growth of filamentous algae, and at the same time reduce viability of foundation species such as *F. vesiculosus*. Experiment and field data yielded complementary information on *F. vesiculosus* temperature and salinity tolerances. In experiments conducted, low salinity increased the negative effects of short-term high temperature on *F. vesiculosus* (Chapter II), whereas the effects of ocean acidification on *F. vesiculosus* were minor (Chapter III). The most important results are outlined in detail below.

### 3.1. EXPECTED EFFECTS IN THE MACROALGAL COMMUNITY (CHAPTER I)

Chapter I identified several processes related to future climate change, which have similar outcomes. The projected salinity decline will affect marine species negatively. Foundation species such as *Fucus vesiculosus* and *Fucus radicans* may be lost from areas of low salinity which become unsuitable, and declining salinity will likely cause their geographic ranges to contract towards south. In the margins of the distribution, the ecosystem functions provided by these species may be diminished, because the structural complexity and primary production are related to the size of *Fucus* plants, which substantially declines under low salinity. In contrast, green algae are relatively resistant to low salinity, and may thus be favoured in the future.

Warming lengthens the growing season, which may promote the growth of macroalgae and primary production in the coastal ecosystems in general and alter phenology. Warming may be harmful for some species which clearly favor cold water, such as *Ceramium tenuicorne* and *Pylaiella littoralis*, while green algae are expected to benefit from warming.

Based on the literature surveyed in Chapter I, the effects of ocean acidification remained elusive, and the number of studies conducted on Baltic species was low. In general, red algae, such as *Furcellaria lumbricalis*, and green, filamentous species such as *Ulva intestinalis* may benefit from OA. Responses of *F. vesiculosus* were divergent some studies indicating positive, some neutral and some negative effects.

In summary, Chapter I identified several processes, which work in the same direction (Fig. 7). Low salinity will negatively affect perennial, marine species such as fucoids, but filamentous green algae are relatively resistant. Green algae are also favored by rising temperatures and coastal eutrophication, which is expected to intensify under climate change through both temperature rise and increasing rainfall and subsequent increases in nutrient discharge. This suggests that in the long run, perennial foundation species will likely decline, and filamentous, fast-growing species, especially green algae, will benefit from the expected environmental changes in the future Baltic Sea.

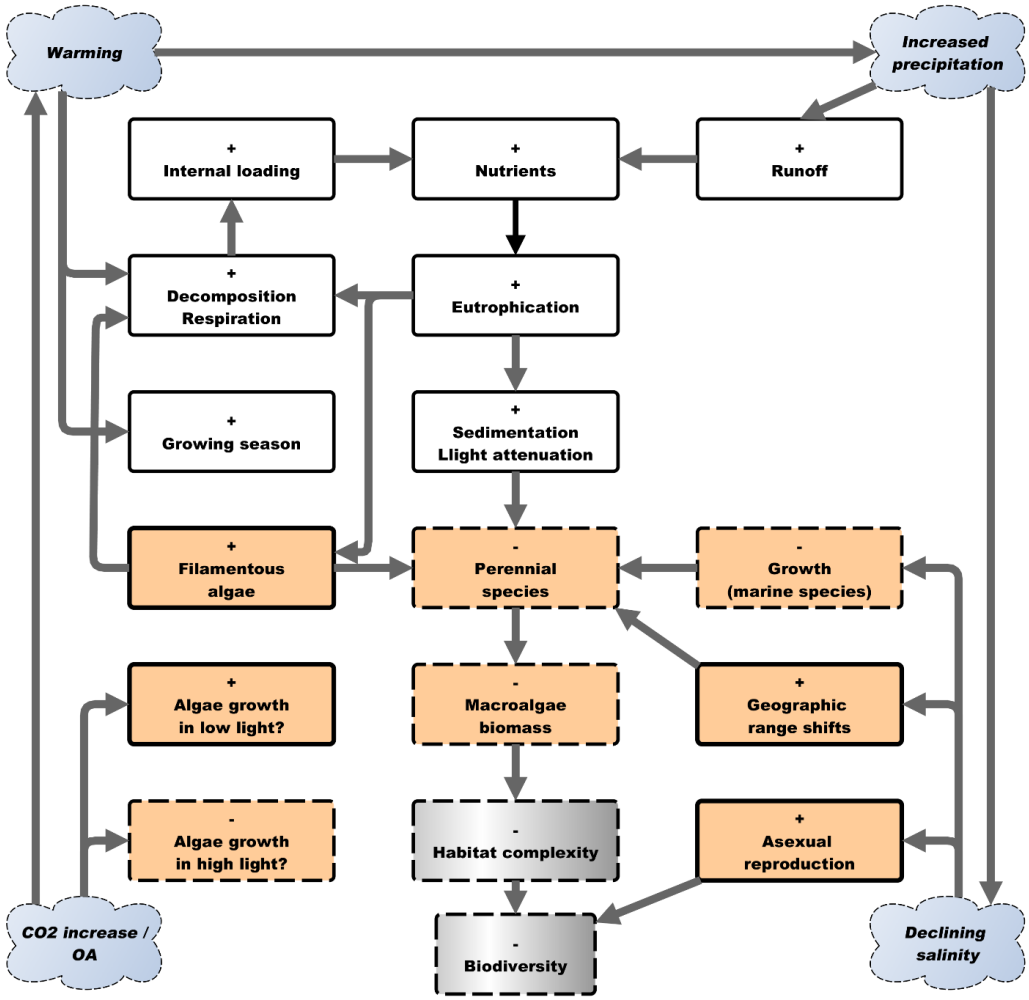


**Figure 7**. Conceptual model of potential effects of climate change in the Baltic Sea macroalgae. Blue clouds indicate abiotic changes brought about by climate change, white boxes indicate ecosystem-level processes, and pink boxes indicate the expected responses in the macroalgal community. Increases in magnitude (positive effect) of a process are indicated by "+" and solid box, decreases in magnitude (negative effect) with a "-" and a dashed box.

## 3.2. THE FUNDAMENTAL NICHE OF *F. VESICULOSUS* (SUMMARY)

The results presented in the following section are an independent analysis and are only presented here in the summary part of the thesis, not in any of the Chapters. The systematic literature search conducted in Chapter I allowed identifying 13 experiments (including the data from Chapter II), from which temperature and salinity responses of *F. vesiculosus* could be extracted (Table 1). The experiments had variable durations and were conducted in different seasons. Most experiments measured growth, which was usually defined as relative growth rate, indicating % of growth per day

(Table 1). In all but one (Steen & Rueness, 2004) experiments, responses on mature vegetative thalli were examined.

**Table 1.** Studies from which experimental data was extracted. Abbreviations: RGR: relative growth rate, FW: fresh weight.

| Reference | Parameter measured | Season | Duration | Temperature (ºC) | Salinity |
|---|---|---|---|---|---|
| Graiff *et al.* (2015) | RGR (% length $day^{-1}$) | April | 21 d | 5 – 27 | 15 |
| Nygård & Dring (2008) | Electron transport rate | February | 7 d | 0 – 25 | 5, 35 |
| Gutow *et al.* (2016) | RGR (% FW $day^{-1}$) | January | 14 d | 10 – 20 | 30 |
| Steen & Rueness (2004) | Growth (zygote area) | June | 15 d | 7, 17 | 25 |
| Werner *et al.* (2016a) | Final biomass | April – September | 90 d | 11 – 24.5 | 15 |
| Wilson *et al.* (2015) | RGR (% FW $day^{-1}$) | June – August | 20 d | 12 – 29 | 32 |
| Werner *et al.* (2016b) | Final biomass | July – August | 60 d | 21 – 26 | 15 |
| Nejrup *et al.* (2013) | Specific growth rate $day^{-1}$ | Summer | 23 d | 10 – 25 | 20 |
| Bäck *et al.* (1992b) | % increase in length | ? | 77 d | 10 | 1.5 – 45 |
| Munda & Hudnik (1988) | % increase in length | August | 21 d | 5 – 15 | 8 - 32 |
| Fortes & Lüning (1980) | % increase in length $day^{-1}$ | March – April | 7 d | 0 – 25 | 35 |
| Chapter II | RGR (% FW $day^{-1}$) | August | 8 (11) d | 20 – 28 | 4, 6 |
| Munda (1977) | % increase in length | March | 6 months | 3 – 15 | 5 – 31 |

The field occurrences of the Baltic *Fucus vesiculosus* covered wide salinity and temperature conditions, with majority of occurrences observed between temperature 13 – 19 ºC and salinity 4 – 8 (Fig. 8a, b). Salinity threshold for *F. vesiculosus* presence was approximately 4 (Fig. 8a, c). *F.vesiculosus* is absent from southeast Baltic Sea due to lack of suitable sites of attachment, although salinity and temperature conditions would allow it to persist. There were no presence or absence observations of *F. vesiculosus* under high temperature and low salinity in the present-day Baltic Sea (Fig. 8c).

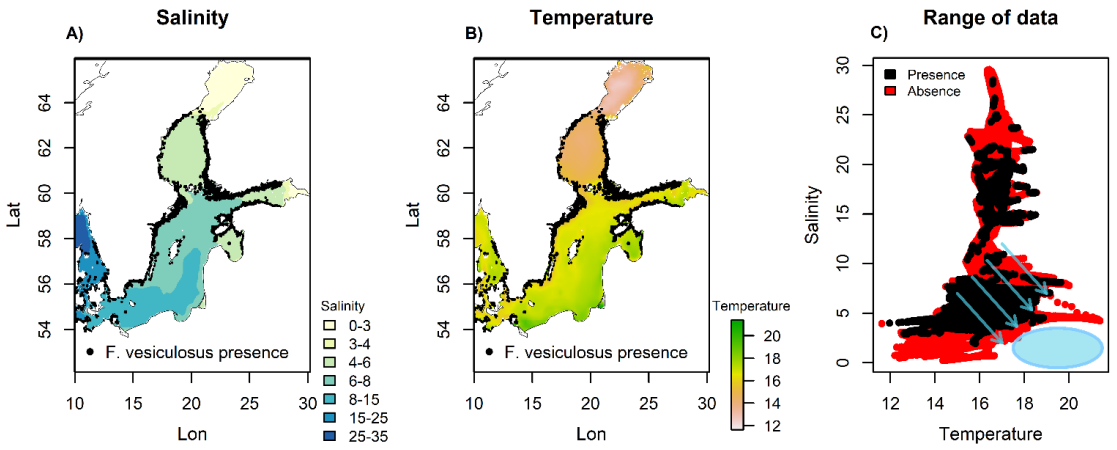


**Figure 8**. Observations of *Fucus vesiculosus* occurrences in the field with mean annual seawater salinity (a), mean temperature of the growing season (JJA, b) and the presences and absences in the field data in relation to temperature and salinity (c). Arrows in the plot (c) show the direction of the expected temperature and salinity changes, and the data range lacking presence or absence observations. Note that *F. vesiculosus* is present also in the North Sea, but in this data set only Baltic observations are included. In the Baltic Sea, *F. vesiculosus* is absent from areas where no presence is shown.

The experimental data obtained through this thesis, on the other hand, covers a substantially wider variable space (Fig. 9), with especially the temperature and salinity values in Chapter II covering the responses to high temperature and low salinity (Fig. 9a).

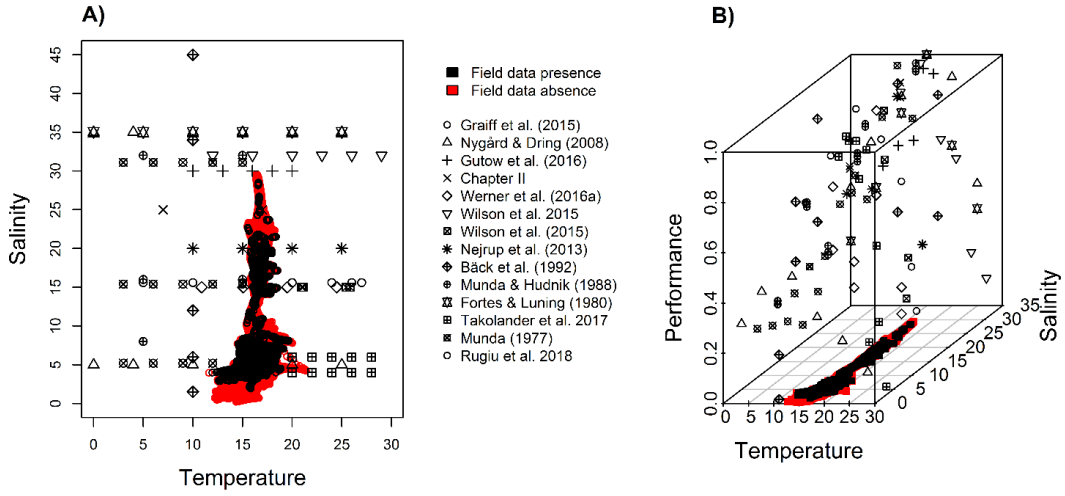


**Figure 9**. Temperature and salinity range of experiment and field data. In b), the parameters measured (Table 1) are scaled between 0 and 1 into a single performance value.

In the experimental data, a declining performance (growth rate in most experiments) along declining salinity was observed, starting from approximately 20 units (Fig. 9b). Similarly, growth also declined steeply in the highest temperatures, after approximately 25 ºC. Based on the experimental data, *F. vesiculosus* has a broad temperature optimum around 15 ºC.

### 3.3. THE IMPORTANCE OF VARIABLE INTERACTIONS (CHAPTERS II AND III)

Rather than the effects of the studied variables alone, it was the variable interactions that were found to be significant, especially the adverse effects of low salinity and short-term high temperature, as identified in Chapter II. On the contrary, the effects of ocean acidification, studied in Chapter III, were not dependent on irradiance.

Chapter II identified an important interaction between short-term high temperature and low salinity on *F. vesiculosus* growth rate. Low salinity significantly added to negative effects of high temperature and caused declines in growth rate. High temperature caused declines in growth rate already in 24 ºC, and substantial tissue necrosis ensued in exposure to 26 ºC (Fig. 10). Low salinity increased tissue necrosis, however, the effect was not observable directly after the heat treatment but only after the 11 days recovery period (Fig. 10b). This highlights the importance of including a period for observing the potential effects that emerge after the treatments have been conducted.

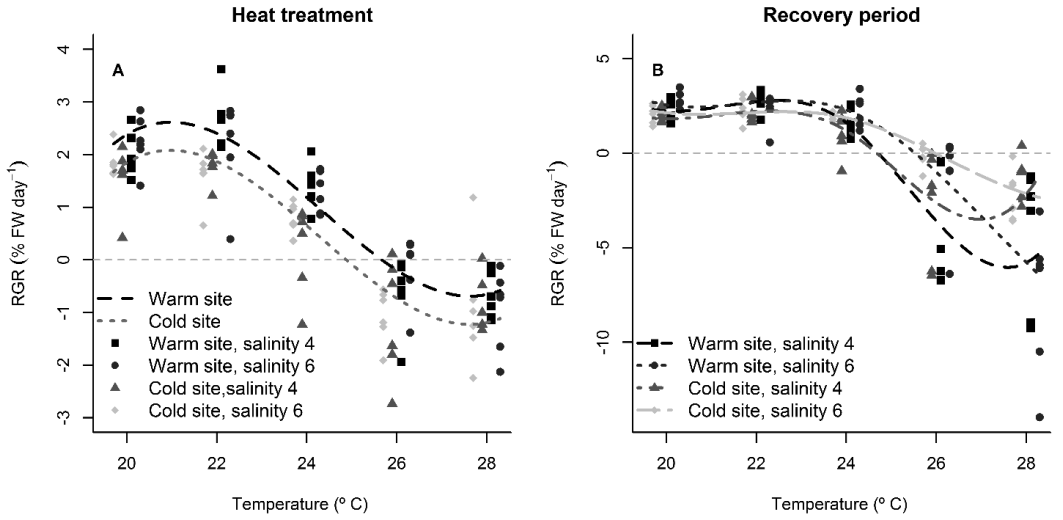


**Figure 10**. Effects of short-term high temperature and salinity (4 or 6) on *F. vesiculosus* growth rate after 8 days of temperature treatment (a) and 11 days of recovery period (b).

The salinity and temperature interaction was not significant in any of the chlorophyll fluorescence parameters measured except steady-state electron transport rate (ssrETR). It was found that the individuals exposed to high temperature and low salinity did not recover the capacity to maintain ssrETR like the individuals in ambient salinity. Individuals from the two local populations showed differences in their responses to temperature. The algae from the warmer site had consistently higher growth rates in all temperatures during the heat treatment (Fig. 10a). There were also differences in

optimal temperature for ETRmax, those from the cold site had optima at 24 ºC, and warm site individuals at 22 ºC.

In contrast to expectations, no evidence for interaction between OA and light was found (Chapter III), i. e. the effects of OA were not dependent on the irradiance the algae were grown in. Growth rate, which can be considered the best performance proxy since it integrates over a range of physiological processes, did not show any response to either irradiance or OA treatments or their combinations. The only parameter measured for which the interaction between OA and irradiance was significant, was maximum potential quantum yield, $F_v/F_m$ in the summer experiment. Under high irradiance, $F_v/F_m$ declined under OA whereas under low irradiance this was not the case (Fig. 11a). The light-limited efficiency of photochemical energy conversion, alpha, showed similar responses (and was marginally significant) (Fig. 11b).

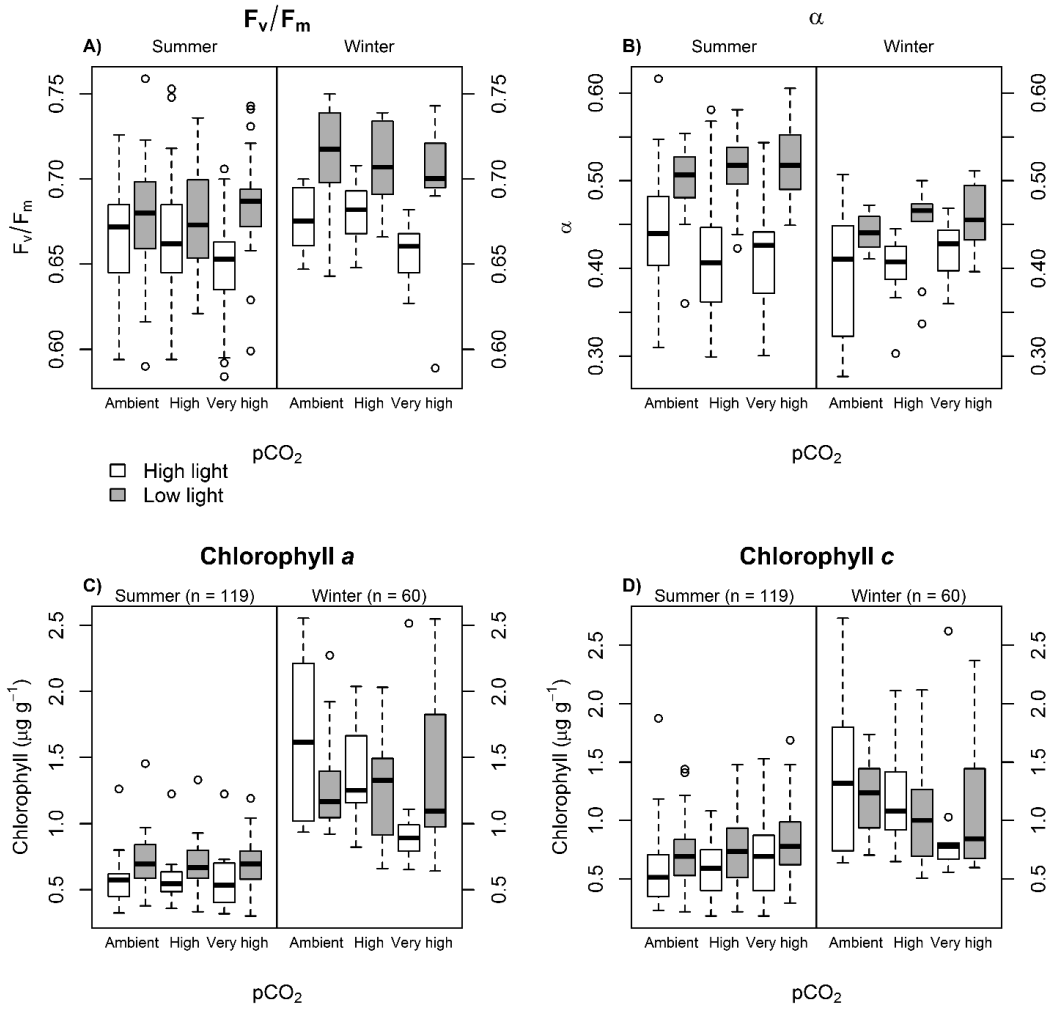


**Figure 11**. Effects of ocean acidification ($pCO_2$ treatment) and irradiance on $F_v/F_m$ (a) alpha (b) and chlorophyll *a* and *c* content (c, d) of *F. vesiculosus*.

3.4. THE EFFECTS OF OCEAN ACIDIFICATION AND SEASONALITY OF RESPONSES (CHAPTER III)

In Chapter III, when the experiments covered two different seasons, all parameters measured showed seasonal patterns. First, when the standardized regression coefficients of the main effects, indicating the magnitude of an effect, were compared, it was found that the effect of season on all parameters measured was greater than those of irradiance or OA treatments (Fig. 12).

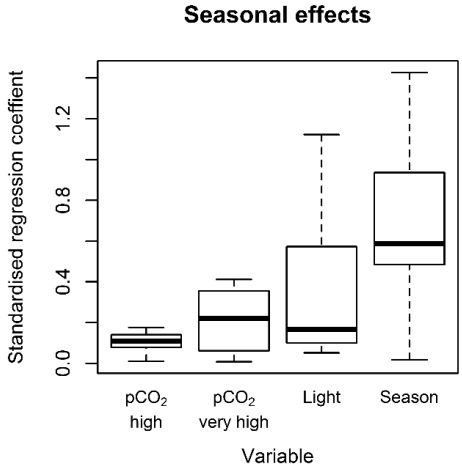


**Figure 12**. Standardized regression coefficients of the main effects of season, irradiance and OA ($pCO_2$) on all parameters measured in Chapter III.

Second, some of the observed responses of *F. vesiculosus* on OA and irradiance treatments were observable only during either of the seasons. For instance, nitrogen content, measured as percentage of dry weight, declined under highest OA treatment, but only during winter. Similarly, C:N ratio and carbon content were elevated by both irradiance and OA treatments, but only in winter (Fig. 13b, d). During winter, the carbon content of *F. vesiculosus* was low, but specimens under high irradiance had a significantly higher carbon content, which was not observed during summer (Fig. 13b). Although responses to OA were observed in several parameters measured in Chapter III, we did not observe any effects on growth rate in either of the experiments (Fig. 13a), which suggests that the direct effects of OA on mature *F. vesiculosus* are likely minor.

In addition to carbon and nitrogen content, also chlorophyll fluorescence parameters and chlorophyll content showed high seasonality. In general, chlorophyll content was more than two times higher during winter (Fig. 11c,d), which is caused by the low light availability the algae have adapted to (Leskinen *et al.*, 1992). Similar patterns were also observed in the chlorophyll fluorescence parameters measured. Winter samples had high values of maximum potential quantum yield ($F_v/F_m$, measured on dark-adapted samples), whereas the differences in actual photochemical energy conversion efficiency (alpha) were not as divergent between the two seasons (Fig. 11a, b).

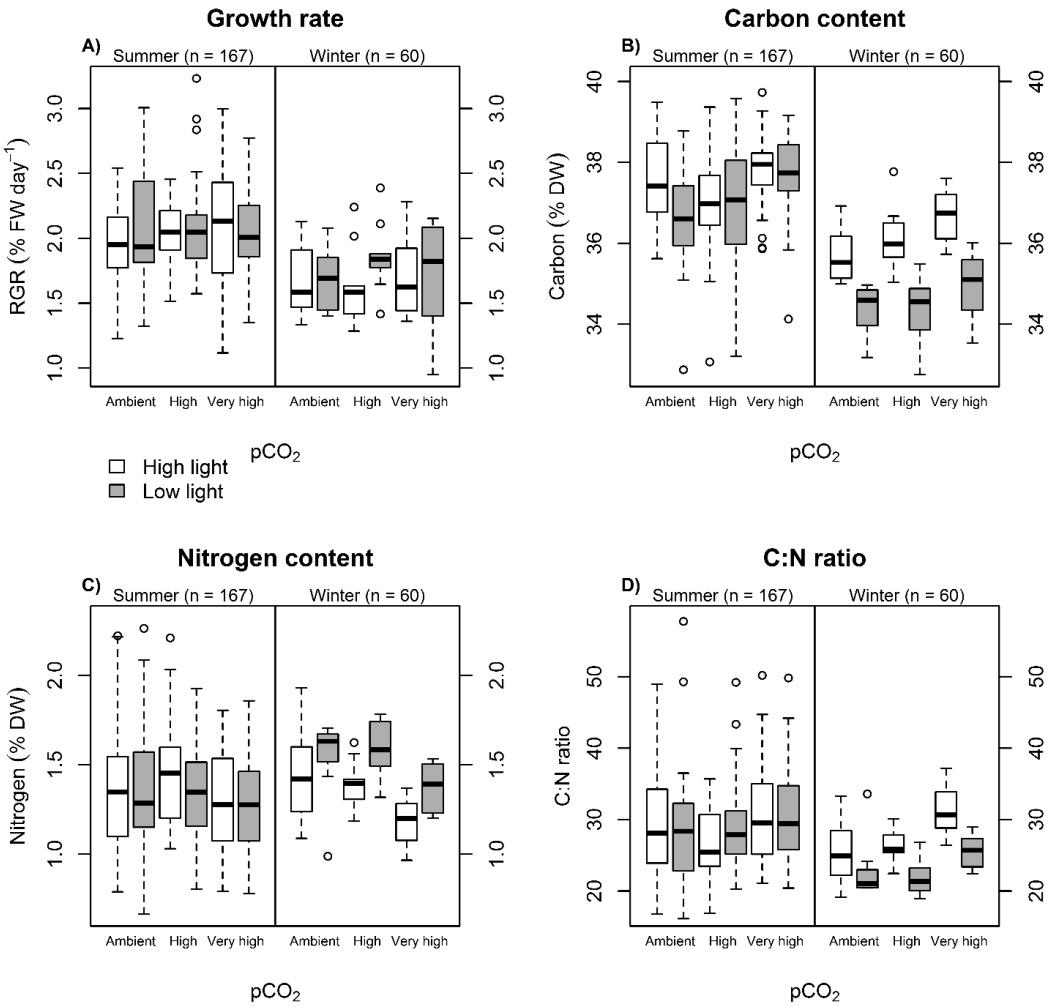


**Figure 13**. Effects of ocean acidification ($pCO_2$ treatments) and irradiance on *F. vesiculosus* growth (a), carbon (b) and nitrogen (c) content and carbon:nitrogen ratio (d).

## 4. DISCUSSION

### 4.1. COMMUNITY LEVEL EFFECTS

Evidence suggests that green algae appear relatively tolerant against declining salinities. Thus, in areas subjected to low salinity in the future, these species may form a substantial part of the macroalgal species pool and biomass. In summer, filamentous algae are important habitats for invertebrate fauna (Kraufvelin & Salovius, 2004), but filamentous algae are annual and cannot provide the amount of year-round persistence of biomass like perennial species such as *Fucus* spp., which indicates that in the long run the diversity of species associated with fucoids may decline.

Some *Fucus vesiculosus* populations have been observed reproducing sexually under relatively low salinity (2 units, Ardehed *et al.*, 2016). This suggests that local populations in the Baltic might have different salinity tolerances, which could allow for some adaptation in future conditions. Rugiu et al. (2018) showed that there is variability in growth responses to future temperature and salinity conditions, both within and between local and regional Baltic *F. vesiculosus* populations, although they found that the overall effects of climate change were negative, despite local differences in responses. However, the reviewed literature in Chapter I suggests that in the future, genetic potential for such adaptation may be reduced, as indicated by the found increase in frequency of asexual reproduction observed under low salinity foe many species.

As identified in Chapter I, increases in temperature may be harmful for some cold-adapted species. Artificial heating in surroundings of nuclear power plants provided glimpses of potential effects on different species. In Forsmark, Sweden, heating by nuclear power plant negatively affected *Ceramium tenuicorne*, *Pylaiella littoralis* and *Chorda filum*, while green algae, especially *Ulva* spp. proliferated (Snoeijs, 1992b). In Finland, artificial heating near nuclear power plants was similarly observed to boost overall primary production, but mostly in eutrophic conditions (Ilus, 2009).

Climate change may enhance eutrophication by increasing nutrient loading from land, increasing internal loading, and through lengthening of the growing season. Effects of eutrophication on macroalgae are well known and include loss of slow-growing perennial species and mass occurrence of drifting filamentous algal mats, which consist of fast-growing species such as *Ulva* spp. and *Pylaiella littoralis* (Bäck *et al.*, 2000).

## 4.2. THE FUNDAMENTAL ABIOTIC NICHE OF *F. VESICULOSUS* AND IMPLICATIONS FOR FUTURE MODELLING EFFORTS

The field observations of Baltic *Fucus vesiculosus* presence and absence used in evaluating the fundamental niche covered wide temperature and salinity gradients. However, in this Baltic distribution data, there were no observations of *F. vesiculosus* presence or absence under low salinity and high temperature, which is the direction of environmental change in the Baltic, according to climate change projections (Meier, 2006; HELCOM, 2013; BACC II Author Team, 2015). If climate change effects on *F. vesiculosus* are evaluated with distribution data only, some responses which are important under future temperature and salinity conditions will likely be missed. This suggests that experimental data is a valuable data source in estimating expected effects of climate change on *F. vesiculosus*.

In the experimental data, temperatures above 25 $^{o}$C had strong negative effects on growth. This was well above the highest temperatures encountered in the field data, which indicates that in the Baltic, the current temperatures do not restrict *F. vesiculosus* occurrence. In contrast, in the Atlantic high seawater temperature has caused range contractions in *F. vesiculosus* southern distribution edge (Nicastro *et al.*, 2013). Given that the Baltic Sea is warming rapidly, the temperature responses extracted from experiments may be used to identify important processes affecting future geographic distribution of the species, even if temperature does not restrict distribution in present day conditions. The experimental data was sampled from experiments conducted in different regions, covering the Baltic Sea, North Sea and the Atlantic. As the Baltic *F. vesiculosus* may be adapted to low salinities and temperatures during recent millennia (Russell, 1988; Bäck *et al.*, 1992a, 1992b), it is possible that the responses obtained from Baltic and Atlantic populations are somewhat different.

It is noteworthy that although the majority of experiments only evaluated the responses of *F. vesiculosus* in monocultures, the results from two mesocosm experiments (Werner *et al.*, 2016a, 2016b) imply that the *Fucus* ecosystem, including grazers and epiphytes, may be more vulnerable to warming than a *Fucus vesiculosus* monoculture. Mesocosm experiments showed, that *F. vesiculosus* biomass declines already substantially at 24 ºC, which is a lower threshold than what was observed when only direct effects on *F. vesiculosus* were investigated in monocultures. The responses arose from steep declines in the biomass of grazers, especially in late summer, which resulted in overgrowth of epiphytic filamentous algae on top of *F. vesiculosus*, eventually leading to sharply declining *F. vesiculosus* biomass. These results suggest that biotic interactions are likely to be altered by climate change, and that incorporating biotic interactions into modelling and other research efforts is important.

In the experiments covered here, parameters concerning the performance of mature, vegetative thalli were investigated. Growth rate is a good performance proxy, as individuals need to maintain a positive growth rate in order to survive in particular environmental conditions. Despite this, the growth responses measured on mature individuals do not necessarily fully reflect the complete abiotic niche of the species, if for example, the geographic range is limited by some other process restricting the completion of a full life cycle. In *F. vesiculosus*, this type of process is seen in the reproductive failure in low salinities (Serrão *et al.*, 1996, 1999). Although we observed declining growth along a declining salinity range, the experiments did not explicitly capture the aforementioned process, which was identified through a systematic literature search in Chapter I. Although this response was not addressed by the growth rate measurements, the process may be integrated into a species distribution model by using e.g. a Bayesian approach, which allows the incorporation of prior information into the model in a formal framework (Gelman *et al.*, 2014). In such case, a decline in performance or total disappearance under certain salinity threshold may be specified into the model as prior information. Thus both quantitative (growth responses) and qualitative (reproductive failure) responses from literature would complement the information obtained from the field data, in a promising framework for building a hybrid species distribution model for *F. vesiculosus*.

Few attempts to include physiological tolerance thresholds in modelling geographic ranges of macroalgae have been made (Martínez *et al.*, 2015; Franco *et al.*, 2018). In both cases, a single experiment was conducted to estimate the temperature tolerance ranges, which were qualitatively compared with geographic distribution projections obtained through an SDM. The approach applied in this thesis, assessing the fundamental niche through interaction of temperature and salinity with both field data and a set of experimental responses derived through a meta-analysis, provides a wider set of responses and treatment levels, and allows to quantify the temperature-salinity interaction based on experimental data.

Experiments and spatial modelling both have their strengths and weaknesses, and a combination of the two could potentially overcome the limitations and become a valuable tool in the future climate change biodiversity research. Experimental manipulations in laboratory experiments could target ranges of environmental ranges not covered by spatial observations of species distributions, to verify that the species investigated occupies the full extent of environmentally suitable niche, and that the spatial model thus truly captures the physiological performance threshold of the species. Experiments may be designed to target the environmental conditions, and their future expected combinations, thus addressing the extrapolation problem, which is one of the major uncertainties of SDMs. This could potentially yield spatial predictions of species' distributions and their expected changes that would be realistic, and rooted in physiological performance, improving the robustness of SDMs.

Earlier modelling approaches regarding *F. vesiculosus* distribution through SDMs have utilized observed distributions (Jueterbock *et al.*, 2013; Leidenberger & Giovanni, 2015; Jonsson *et al.*, 2018), which means that the models used need to extrapolate outside the existing range of calibrating field data to create predictions for the future, especially in the Baltic Sea. Extrapolation to novel environmental conditions is one of the main uncertainties of SDM methodology (Elith & Graham, 2009; Fitzpatrick & Hargrove, 2009). Since salinity has such a strong influence on Baltic species distributions (Hällfors *et al.*, 1981; Nielsen *et al.*, 1995; Bergström & Bergström, 1999; Schubert *et al.*, 2011), it is inevitably the single most important factor in modelling efforts. Although the models applied probably capture correctly the response to low salinity in the field data (Jonsson *et al.*, 2018, but see Leidenberger & Giovanni, 2015), salinity-temperature interaction in future conditions (under high temperature and low salinity) cannot be reliably estimated from the field data simply because such conditions do not exist under present climate. The results in Chapter II indicate that the interaction is important and should be included in modelling efforts. This importance is further highlighted when the observed warming (MacKenzie & Schiedek, 2007; Belkin, 2009) and expected increases in frequencies of extreme temperatures (Neumann *et al.*, 2012) are taken into consideration.

## 4.3. VARIABLE INTERACTIONS

Chapter II identified the importance of including variable interactions, especially regarding temperature and salinity, which are the vitally important variables expected to change in the future (BACC Author Team, 2008; BACC II Author Team, 2015). Chapter II showed that under the low salinity expected to occur in the Northern Baltic in the future, the effects of short-term heat waves on *F. vesiculosus* are more severe. The results indicate that under ambient summer seawater temperature (~20 ºC) salinity of 4 does not impose negative effects on *F. vesiculosus*, at least under short-term exposure. This may not hold, however, under longer exposure times. Temperature of 20 ºC and salinity of 4 were observed to reduce growth rate of central Baltic Sea *F. vesiculosus* dramatically (Rugiu *et al.*, 2018), when experiments were run for 140 days. Thus it is important to note, that both experiments addressing the effects of short-term extreme events and the effects of long-term changes in the mean conditions are needed to build a comprehensive picture of the expected future impacts of climate change on *F. vesiculosus*.

In Chapter III, the only parameter affected by the interaction between OA and light was $F_v/F_m$. Since the maximum electron transport rate and chlorophyll content did not follow this pattern, the implication is either a dynamic downregulation of the efficiency of light-limited energy capture (by definition alpha and $F_v/F_m$ are highly correlated), or a modest level of photoinhibition. Photoinhibition, a decline in photosynthetic efficiency, may be caused by visible light, in which case photoinhibition in the light-limited photosynthetic capacity ensues before the effects are observed in light-saturated state, which is followed by oxidative damage and bleaching of photosynthetic pigments (Powles, 1984). As no pigment bleaching or photoinhibition under light-saturated state (rETRmax) was observed, the potential effect of photoinhibition appears minor. Alpha and $F_v/F_m$ indicate the efficiency of energy conversion in low irradiances, and it is also possible that the algae did not maintain high capacity under excessive carbon and light, because they could acquire satisfactory levels of carbon with lower investments.

Variable interactions are often neglected in climate change studies (Wernberg *et al.*, 2012b), despite their obvious ecological importance (Wahl *et al.*, 2011). One of the limitations in including interactions into experiments is the increase in the number of replicates, as interactions, especially

with multiple treatment levels, as in Chapter II, quickly expands the size of the experiment. This often reduces either number of replicates per treatment level or combination of levels, which may reduce the statistical power of experiment, causing only strong interactions (large effect sizes) to be identified. In Chapter II, the statistical significance of low salinity and high temperature interaction could be observed even with a relatively low number of replicates (N = 6). On the contrary, potentially due to relatively minor effects of OA and irradiance, no interaction was found in Chapter III, despite substantially larger number of replicates N = 10/30, winter/summer).

Including interactions may increase the ecological realism of the experiments, making possible e.g. to include seasonal patterns in confounding factors into experiments (e.g. Franco *et al.*, 2018). Chapter II allowed to evaluate this type of process through combining a seasonally fluctuating variable (temperature) with another with modest seasonal fluctuations (salinity). The results indicate that inferences based on only single factor manipulations may not capture the full range of responses expected under multiple dimensions of climate change, which emphasizes the importance of identifying responses against interacting factors.

## 4.4. OCEAN ACIDIFICATION AND SEASONALITY OF RESPONSES

*Fucus vesiculosus* has been shown to store carbon and nitrogen internally over seasons (Lehvo *et al.*, 2001), taking up nitrogen during winter, and utilizing the internal reserves in summer when external nitrogen concentration in seawater is low which a general adaptive trait of large brown macroalgae, such as kelps (Dring, 1992). In this study, the nitrogen content in algal tissue declined under OA in winter, which suggests that the temporal pattern of nitrogen accumulation may be disrupted under OA. In the OA treatments during winter, *F. vesiculosus* plants had a greater carbon content, especially under high irradiance, suggesting that photosynthesis rates were stimulated by OA treatments, even though this response was not captured in chlorophyll fluorescence measurements. In winter, the tissue carbon content was substantially lower than during summer. The algae may have utilized the storage carbon for growth during winter, when photosynthesis rates in their natural setting are low (Lehvo *et al.*, 2001). In contrast, during summer, the OA treatments did not stimulate carbon accumulation notably, since the algae already had high carbon reserves, likely in the form of mannitol, which is the main carbon storage compound and sink for photosynthetically acquired carbon in *F. vesiculosus*. If, as indicated by these results, *F. vesiculosus* can increase its carbon storage during the winter due to OA, this may result in potentially more rapid growth and onset of reproduction during spring, both of which have already been shown to be stimulated by increasing temperature and light availability (Kraufvelin *et al.*, 2012).

Earlier studies on the effects of OA on *F. vesiculosus* have shown negative (Gutow *et al.*, 2014) or slightly positive (Al-Janabi *et al.*, 2016b; Werner *et al.*, 2016a) effects on growth during the summer growing season. The negative effects in growth during winter (Gutow *et al.*, 2014) were observed with much more conservative $pCO_2$ treatments than applied in Chapter III. Previous experiments have also identified that the magnitude of OA effects are much smaller than those of elevated temperature (Werner *et al.*, 2016a). It is thus possible that a positive effect of OA on *F. vesiculosus* growth exists, but the experiments in Chapter III were not able to capture it, potentially due to limited duration (~3 weeks) of both experiments.

An increase in the carbon content of algae, especially in winter, may indicate an increase in using $CO_2$ for photosynthesis, which has been observed in macroalgae able to use both $HCO_3^-$ and $CO_2$ as carbon source in field conditions with high $pCO_2$ (Cornwall *et al.*, 2017). Isotope ratios ($^{12}C$:$^{13}C$,

abbreviated $\delta^{13}C$) can be used in identifying CCM activity in macroalgae (Raven *et al.*, 2002). In our study, however, the $\delta^{13}C$ values were not measured, and thus the CCM downregulation under OA treatments remains speculative. The energetic gain through downregulation of CCM may emerge from downregulation of CCM activity or CCM maintenance and upkeep (Raven *et al.*, 2014). If majority of energy savings are gained through downregulating the upkeep of CCM, the potential effects might emerge only after certain period of acclimation or adaptation over several generations.

The differences in responses observed here between the two seasons highlight the importance of considering seasonal variations in experimental setting. Natural variability in temperate coastal environments such as northern Baltic is high, and should be included in experimental designs to acquire more robust inferences (Wahl *et al.*, 2016). The effects of OA on primary producers depend on both species physiological adaptations to seasonal changes, and the magnitude of OA in the Baltic Sea system in general. Many of the experiments conducted on OA effects on macroalgae have investigated only responses during a single season (e.g. Gutow *et al.*, 2014; Celis-Plá *et al.*, 2015; Fernández *et al.*, 2015; Iñiguez *et al.*, 2015; Nunes *et al.*, 2015; Rautenberger *et al.*, 2015) (but see Al-Janabi *et al.*, 2016b, 2016a). The relative importance of seasonal effects may be smaller in study systems which have smaller seasonal variations, such as the tropics, but in temperate and arctic ecosystems seasonal changes in macroalgae physiology may be substantial, due to alterations in environmental factors and algal phenology which has linked to these fluctuations (Wiencke, 1990; Le Lann *et al.*, 2012).

Although we kept the pH of the OA treatments stable between the summer and winter experiments, the seasonal fluctuations in temperature, salinity and alkalinity of the inflowing seawater caused the dissolved $CO_2$ concentration in the summer experiment to be substantially lower than that of the winter experiment. Thus some of the observed differences here attributed to seasonal changes in physiology, especially in parameters which show higher effects of OA in winter, may arise from different $pCO_2$ treatment levels between the two experiments, and therefore the results should be interpreted with caution. The Baltic Sea has high natural seasonal fluctuations in pH and $pCO_2$ of seawater (Omstedt *et al.*, 2009; Schneider, 2011), with $pCO_2$ levels rising in winter and declining in summer due to primary production. This means that generally, fluctuating pattern in $pCO_2$ concentrations also occurs in natural settings.

Some of the seasonal patterns observed in Chapter III may arise from the temperature differences in the two experiments, strongly affecting algal metabolism (Eggert, 2012). Because the experiments were conducted using an indoors flow-through system, the seawater temperature in the field could not be fully replicated. The mean temperature during the experiments was 13.5 $^{o}$C (summer) and 9.1 $^{o}$C (winter). In 2016, the seawater temperature in Längden sampling site in the open sea area outside TZS was 14.5 $^{o}$C in June and 2.0 $^{o}$C in December (FMI, 2016). This indicates that especially the temperature in the winter experiment was much higher than the expected field values. As temperature affects algal metabolism, this may mean that the effects observed in winter experiment (which also had high $pCO_2$ levels) may not fully be realized under OA in the future.

Similarly, it is possible that the light treatments applied were too conservative (i.e. the difference between winter and summer experiments too small) in relation to natural variability. The light levels in the summer experiment correspond to light levels at approximately 3 meters depth and the winter light levels at 0.5 m (Lindström, 2000), which means that in the winter experiment the light levels may have been high compared to conditions in average growing depth of *F. vesiculosus* (Bäck & Ruuskanen, 2000).

It is noteworthy that the effects observed in Chapter III, especially in relation to carbon and nitrogen content in winter, emerged after three weeks under relatively high $pCO_2$ levels. In both cases, the largest effects were observed under the highest $pCO_2$ treatment. Even so, the changes induced by this treatment were relatively small. Stochastic upwelling events may bring $CO_2$-enriched water close to surface, and cause local declines in pH (Saderne *et al.*, 2013). Events like this may become more frequent in the future (Melzner *et al.*, 2013), if oxygen conditions of the Baltic deteriorate as predicted (Neumann *et al.*, 2012). Even so, it is not certain that a stochastic upwelling of $CO_2$-enriched water would persist for the duration applied here, and thus the effects observed regarding the alterations in carbon and nitrogen content may not be realized *in situ*, at least not in magnitudes observed under the highest OA treatment levels applied in Chapter III. The relatively small effects of OA at high $pCO_2$ treatment levels support earlier conclusions that potential positive effects of OA on *F. vesiculosus* may exist, but they are likely to be small (Al-Janabi *et al.*, 2016b; Werner *et al.*, 2016a), at least compared to effects of other environmental factors such as temperature and light availability. Despite potentially too conservative seasonal differences in temperature and irradiance, the large effect of season compared to irradiance or OA supports the conclusion that the effects of OA on *F. vesiculosus* are minor.

# 5. CONCLUSION AND FUTURE PROSPECTS

This thesis has provided important insights into the responses of Baltic macroalgae to climate change. The most important findings are summarized as follows.

## 5.1. SUGGESTIONS FOR IMPROVING RESEARCH ON CLIMATE CHANGE EFFECTS ON SPECIES

Comparing experimental and field data has allowed the evaluation of the tolerance thresholds controlling the distribution of *F. vesiculosus*. This is a fruitful setting for building an ecologically realistic species distribution model, which can be parameterized to include physiological tolerance thresholds or biotic interactions identified as significant in literature through a meta-analysis. This type of approach may be valuable not only to marine biologists, but it is also applicable to other species and ecosystems, where species range shifts are investigated, and allows addressing the specific responses of a species to variable combinations not encountered under the current climate.

Chapter II highlighted the importance of including variable interactions in experimental designs. In addition, some of the responses were observable only after a recovery period. The two local populations sampled had somewhat differing responses to temperature treatments. Recommendations based on this study include: 1) when conducting experiments with stressful treatments, a monitoring period should be included after the treatment to ensure that all relevant responses are captured; 2) when possible, responses of several local populations should be investigated; 3) variable interactions should be included when possible to strengthen the ecological realism of experiments.

Chapter III identified the importance of seasonality. To fully capture the expected effects of climate change, experiments should be conducted in or should span multiple seasons. This is especially important in temperate and arctic ecosystems, where seasonal changes in environmental conditions are large.

## 5.2. THE MOST IMPORTANT INSIGHTS ON BALTIC SEA MACROALGAE AND CLIMATE CHANGE

Declining salinity, increasing temperature, intensifying coastal eutrophication and ocean acidification appear to have similar outcomes, by increasing the abundance of filamentous algae, already favoured by the coastal eutrophication. At the same time, the expected consequences of these processes for perennial foundation species such as *F. vesiculosus* are negative and indicate that the ecosystem functions provided by these might be lost from large areas.

The experiments in this thesis identified that even short exposure to high seawater temperature has strong negative effects on *F. vesiculosus*, when coupled with exposure to the expected future low seawater salinity levels. This indicates that in the northern Baltic, *F. vesiculosus* populations residing in shallow, sheltered locations which may be subjected to short-term heat waves in the future will be especially vulnerable.

Effects of ocean acidification on *Fucus vesiculosus* are minor. Ocean acidification may have slightly positive effects on *F. vesiculosus* growth in the form of increased carbon availability and storage, but the magnitude of the effect is small in comparison to other environmental effects such as irradiance. Large seasonal changes in *F. vesiculosus* ecophysiology were observed, and the magnitude of seasonal effects far outweighed those of ocean acidification treatments.

Climate change may intensify the effects of coastal eutrophication and increase the abundance of filamentous green algae, which already are favoured by the eutrophication problem. This emphasizes the importance of controlling nutrient emissions, which is a feasible climate change adaptation strategy for the Baltic Sea. As climate change has been predicted to increase nutrient run-off through increasing precipitation, more ambitious reductions in nutrient emissions are needed in all Baltic countries.

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